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Coral biodiversity from Morocco after the End-Triassic mass extinction

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Abstract – Each new coral-bearing outcrop found in Lower Jurassic strata is useful to understand the evolution of corals between the end-Triassic mass extinction and the Toarcian anoxic event. Here we provide new taxonomic data on corals issued from fieldwork on four outcrops from the region of Amellagou, in the High Atlas Mountains, Morocco. A set of 157 coral specimens have been collected from a small biostrome, a giant reef and two olistholiths, spanning from Hettangian – Sinemurian time interval to early Pliensbachian. These corals are distributed in 14 families, 22 genera and 27 species. Among these species, two are new: *Lepidophyllia (Heterastraea) microcalix* sp. nov., represented enough to allow a population study and *Paracuifia castellum* sp. nov. The study extends the last appearance datum of several genera known only in the Triassic till now, namely: *Parastraeomorpha, Araiophyllum, Paracuifia, Pinacophyllum* and, possibly, *Paravolzeia*. For this reason, the severity of the end-Triassic mass extinction is questioned in comparison to the extinction events that happened around the Pliensbachian-Toarcian boundary. For this reason, moreover, the phyletic discontinuity between some Triassic and Jurassic taxa is also addressed. Some Lazarus taxa known from Triassic and Pliensbachian remain absent in Hettangian and now, at a lesser degree, in Sinemurian. That is why we assume that the absence of these taxa is only due to the poor preservation of coral environments during these times. This study also changes our view on the first appearance datum of several genera that were known in Jurassic strata, namely*: Proleptophyllia, Vallimeandropsis* and, possibly, *Lochmaeosmilia.* A special attention is given to the distribution of colonial arrangements and points to the important proportion of cerioid and solitary corals. Additionally, the study highlights the existence of significant proportions of thamnasterioid and meandroid forms. The presence of corals with such a level of integration, together with the occurrence of two species that show platy to ramose transition in their colony shape, namely *Hispaniastraea murciana* and *Chrondrocoenia clavellata*, stresses the effectiveness of a photosymbiosis in these Early Jurassic coral communities. Lastly, the proportion of solitary specimens increased over time, revealing the uniqueness of coral assemblages during the Pliensbachian.

Keywords: Scleractinia / Morocco / Early Jurassic / extinction / biodiversity / recovery

Résumé – Biodiversité corallienne du Maroc après l'extinction de masse du Trias-Jurassique. Chaque nouvel affleurement corallien découvert dans les strates du Jurassique inférieur est utile pour comprendre l'évolution des coraux entre l'extinction de la fin du Trias et l'événement anoxique du Toarcien. Nous fournissons ici de nouvelles données taxinomiques sur des récoltes de coraux issues de travaux de terrain sur quatre affleurements de la région d'Amellagou, dans les montagnes du Haut Atlas, au Maroc. Un ensemble de 157 spécimens de coraux a été collecté provenant d'un petit biostrome, d'un récif géant et de deux olistolithes s'étendant de l'intervalle de temps Hettangien –Sinémurien au Pliensbachien inférieur. Ces coraux sont répartis en 14 familles, 22 genres et 27 espèces. Parmi ces espèces, deux sont nouvelles, *Lepidophyllia (Heterastraea) microcalix* nov. sp., suffisamment représentée pour permettre une étude de population et *Paracuifia castellum* sp. nov. L'étude étend la dernière apparition de plusieurs genres connus jusqu'à présent seulement dans le Trias, à savoir : *Parastraeomorpha, Araiophyllum, Paracuifia, Pinacophyllum,* et peut-être *Paravolzeia*. Pour cette raison, la sévérité de l'extinction de la fin du Trias est remise en question par rapport aux événements d'extinction qui se sont produits autour de la limite

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Pliensbachien-Toarcien. Pour cette raison aussi, la discontinuité phylétique entre certains taxons du Trias et du Jurassique est également remise en question. Des taxons Lazare connus du Trias et du Pliensbachien restent absents dans l'Hettangien et maintenant à un moindre degré dans le Sinémurien. C'est pourquoi nous supposons que l'absence de ces taxons est uniquement due à la mauvaise préservation des milieux coralliens à ces époques. L'étude change notre point de vue sur la date de première apparition de plusieurs genres qui étaient connus dans les strates jurassiques, à savoir : *Proleptophyllia, Vallimeandropsis*, et peut-être *Lochmaeosmilia*. Une attention particulière est accordée à la distribution des arrangements coloniaux et souligne la proportion importante de coraux cérioïdes et solitaires. De plus, l'étude souligne l'occurrence de proportions non négligeables de formes thamnastérioïdes et méandroïdes. La présence de coraux avec un tel niveau d'intégration, ainsi que l'occurrence de deux espèces qui montrent une transition lamellaire à rameuse dans la forme de leur colonie (*Hispaniastraea murciana* et *Chondrocoenia clavellata*), indiquent l'efficacité d'une photosymbiose dans ces communautés coralliennes du Jurassique inférieur. La proportion de spécimens solitaires a augmenté avec le temps, ce qui indique la singularité des assemblages coralliens au cours du Pliensbachien.

Mots clés : Scleractinia / Maroc / Jurassique inférieur / extinction / biodiversité / récupération

1 Introduction

The beginning of the Early Jurassic is classically considered a difficult time for corals and therefore for reefal ecosystems in which corals have always played an important role throughout the Phanerozoic. This epoch was even referred to a "reef gap" (Flügel and Kiessling, 2002) or more softly to a "reef eclipse" (Stanley, 1992, 1997, 2001). The reality is that this period of reef disturbance occurs between two extinction events. Corals faced a first severe extinction at the end of the Triassic (Kiessling *et al.*, 2007; Lathuilière and Marchal, 2009), then a second severe multiphased extinction at the end of the Pliensbachian (Vasseur *et al.*, 2021). Consequently, the discovery of new coral records in the Hettangian, Sinemurian and Pliensbachian is still important for understanding corals evolution. The literature of course mentions corals in the Early Liassic for a long time in Western Europe (Orbigny, 1850; Martin, 1860; Dumortier, 1864; Fromentel and Ferry, 1865–1869; Duncan, 1865–1868; Terquem and Piette, 1868; Tomes, 1878, 1884a, 1888, 1893; Nicklès, 1902; Hahn, 1911; Joly, 1936). Part of these anciently known corals were revised by Alloiteau (1957) and Beauvais (1976) but new investigations have been undertaken more recently (Turnšek *et al.*, 1975; Simms *et al.*, 2002; Kiessling *et al.*, 2009; Gretz *et al.*, 2013, 2014; Gretz, 2014; Boivin *et al.*, 2018). Early Jurassic corals have also been collected in Eastern Europe (Popa, 1981; Turnšek and Buser, 1999; Turnšek and Kosir, 2000; Turnšek *et al.*, 2003), and a rather diverse fauna has been described from Central Asia (Melnikova, 1972, 1975a, 2006; Melnikova *et al.*, 1993; Melnikova and Roniewicz, 2012, 2017) a part of which has been very recently reassigned to younger strata (Melnikova and Roniewicz, 2021).

Even if Lower Jurassic corals were also described from South America (Tilmann, 1917; Gerth, 1926, 1928; Wells, 1953; Prinz, 1991) and North America (Poulton, 1988; Stanley and McRoberts, 1993; Stanley and Beauvais, 1994; Hodges and Stanley, 2015), overall this is a difficult time for corals!

Africa has been poorly represented for a long and after some preliminary reports (Le Maître, 1935, 1937) the historical work of Beauvais (1986), devoted to the Liassic coral fauna of Morocco, appeared to be a keystone in our understanding of the group. However, the collection was mostly done in the Pliensbachian and Toarcian stages. Consequently, we undertook to revisit the field in Morocco taking advantage of the recent work of C. Durlet (unpublished), Sarih (2008) and Sarih *et al.* (2018) in the Amellagou region to investigate the Lower Jurassic successions.

Our recent fieldworks in Morocco, between 2014 and 2019, has already resulted in papers devoted to specific abundant taxa such as *Hispaniastraea* (Turnšek and Geyer, 1975; Boivin *et al.*, 2019) and *Neorylstonia* Vasseur *et al.*, 2019. This paper aims to establish a more complete record of early Liassic post-extinction corals. Following recent contributions involving European countries (Gretz *et al.*, 2013, 2014; Boivin *et al.*, 2018), the Moroccan outcrops in a favourable paleolatitudinal location offered a compelling opportunity to improve our knowledge of coral communities after the end-Triassic mass extinction.

2 Material and methods

A collection of coral specimens (157 samples) has been collected in the Amellagou region in the Moroccan High Atlas Mountains (Fig. 1). The material sampled is sourced from four Lower Jurassic outcrops presented in Table 1 and detailed below: the Dromedary biostrome (?Hettangian–Sinemurian), the Serdrar reef (upper Sinemurian), the Castle olistolith (upper Sinemurian or lowermost Pliensbachian) and the Owl olistolith (lower Pliensbachian).

In the field, benthic macrofossils were collected extensively, to obtain a complete survey of each reef outcrop. Samples were extracted with a hammer and chisel as well as with a battery-powered angle grinder, when necessary. The material was then photographed and studied under a reflected light stereomicroscope (Wild M5A). They were then cut and polished to obtain thin transverse and longitudinal sections of 70 μm thickness, and of 24 by 36 mm or of 40 by 50 mm as appropriate.

The samples were numbered according to the following code: the initials "SB" (for Simon Boivin) followed by a number given directly in the field (*e.g.*, SB–133). Each piece collected sample is identified by a unique number (*i.e.*, no batch including several samples). Thin sections made from the samples are identified by a letter next to the sample number

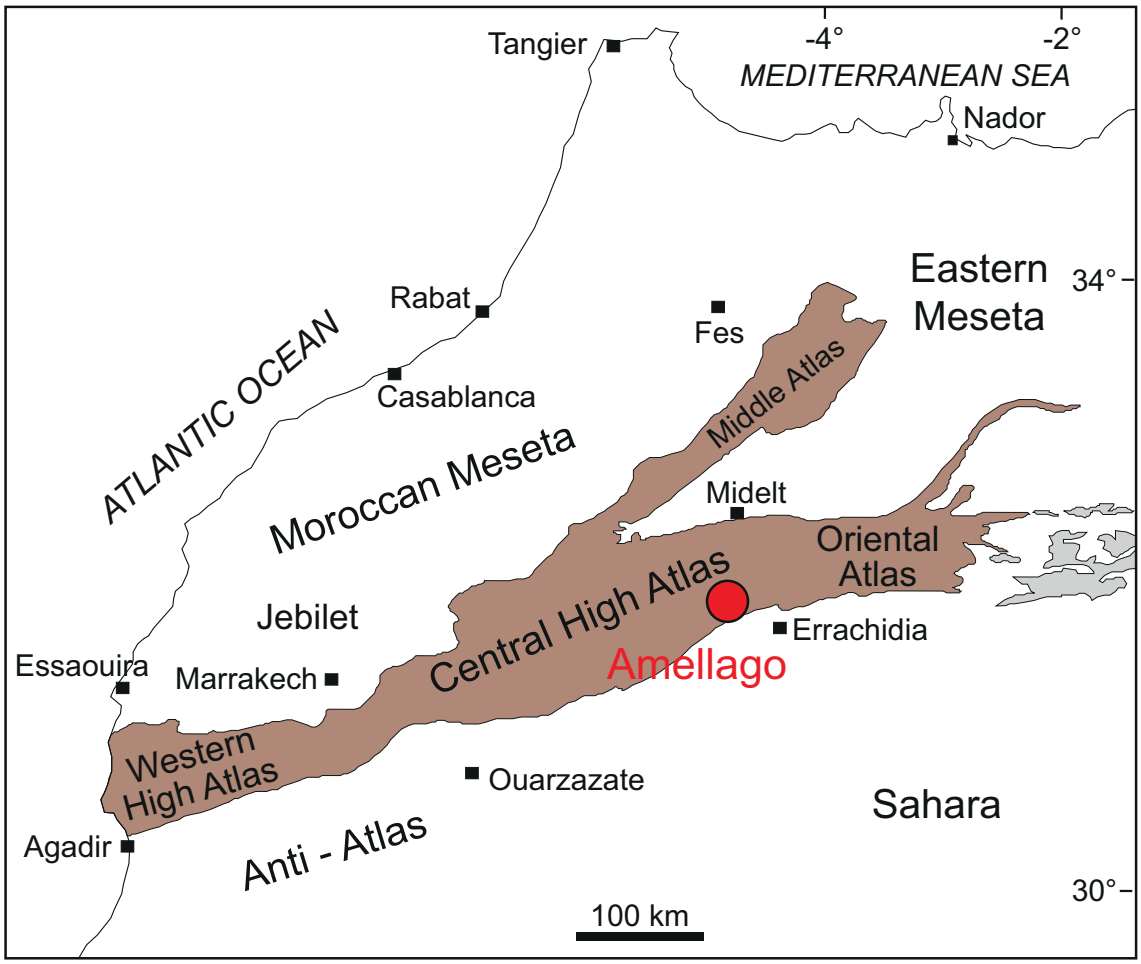

Fig. 1. Map of the main structural domains of Morocco with location of Amellagou Region in High Atlas Mountains. Modified after Krencker *et al.* (2014).

(*e.g.*, SB–133-a). In many cases, different coral species are included in the same sample. To distinguish them, a number preceded by a slash has been added (*e.g.*, the specimens SB–133/1 and SB–133/2).

The silicified corals were extracted with hydrochloric acid. As the matrix is calcareous and the silica is not affected by HCl, the samples were immersed in acid (30%). The corals are thus isolated without their matrix.

The samples were studied mainly from thin sections due to their preservation, which is often strongly eroded over their entire natural surfaces. The thin sections are studied and imaged using a polarised microscope and a thin-section scanner. The description of the coral specimens was carried out following the exhaustive list of observable coral characters proposed by Beauvais *et al.* (1993); a re-structured version is available in Bertling (1995).

In the aim to study the morphometry of coral specimens, several measurements were taken thanks to a calliper or under a microscope with calibrated measurement software depending on the dimensions of specimens. Table 2 presents the different measurements made, also shown in a schematic representation in Figure 2. Depending on the morphology, the colonial structure and the preservation of the material, not all measurements could be taken.

The R software package was used to process the measurements and analyses (R Core Team, 2017) with the libraries ggplot2 (Wickham, 2009) for plots and iNext (Chao *et al.*, 2014) for rarefaction curves. When sampling is large enough, the morphometric data were analysed with several Principal Component Analyses (PCA) with variance/covariance matrices. PAST software (Hammer *et al.*, 2001) was also frequently used to visualize the data. All data are available in the appendices.

Presently, the samples are deposited at the Muséum d'Histoire Naturelle of Geneva, Switzerland. In the future, they should be redeposited at the Direction de la Géologie, Ministère de l'Énergie, des Mines et du Développement Durable – Département de l'Énergie et des Mines (here abbreviated to DGR), in Rabat, Morocco.

3 Systematics & results

Taxonomic names and synonymies are formulated according to the conventions proposed by Matthews (1973) and open nomenclature is used according to Bengtson (1988). Thus, synonymies are commented on using the following signs placed before the binoma:

Table 1. Summary table of outcrops sampled in the Amellagou Region, High Atlas Mountains, Morocco.

Outcrop	Stage & ammonite chronozone	Depositional environments represented	Coordinates	References
Dromedary biostrome	?Hettangian–Sinemurian	A coral biostrome (2.5 m thick), autochthonous and not reworked, composed of silicified corals included in a mudstone matrix. It is sealed by mudstone to wackestone limestones with abundant black cherts.	N 31.92705 W 4.99234	Sarih (2008)
Serdrar reef	Upper Sinemurian End at Oxynotum Chronozone	A pinnacle coral reef (220 m high), located in an open marine environment on a tilted block head, drowned during the Sinemurian (Oxynotum to Raricostatum Chronozones) and progressively capped by lower offshore deposits.	N 32.0075 W 4.9453	Sarih (2008); Lachkar *et al.,* (2009); Pascault (2018)
Castle olistolith	Upper Sinemurian or lowermost Pliensbachian	Olistoliths corresponding to decametric-scale coral bioherms that initially developed on the platform margin but large blocks cracked off and were redeposited in deeper water. These olistoliths are now embedded in hemipelagic limestones and marls interstratified with calciturbidites and slump deposits.	N 31.9414 W 4.9585	Sarih (2008); Sarih *et al*., (2018) Stone *et al*., (2022)
Owl olistolith	Carixian (lower Pliensbachian) Transition from Ibex to Davoei Chronozones)		N 31.9334 W 5.0019	

Table 2. Main measurements made on coral specimens.

Measurement	Unit	Remark
Calicular great diameter	mm	greater diameter of the calice
Calicular small diameter	mm	taken perpendicularly to the great diameter
Calicular diameter	mm	taken when great and small diameters are unavailable
Distance from corallite to corallite	mm	
Thickness of the wall	mm	
Number of septa	number	
Septal density	number per mm	counted along the wall
Trabecular density	number per mm	rarely available
Distance between trabecular axes	μm	rarely available
Valley width	mm	only for meandroid corals
Colline width	mm	only for meandroid corals
Diameter of branches	mm	

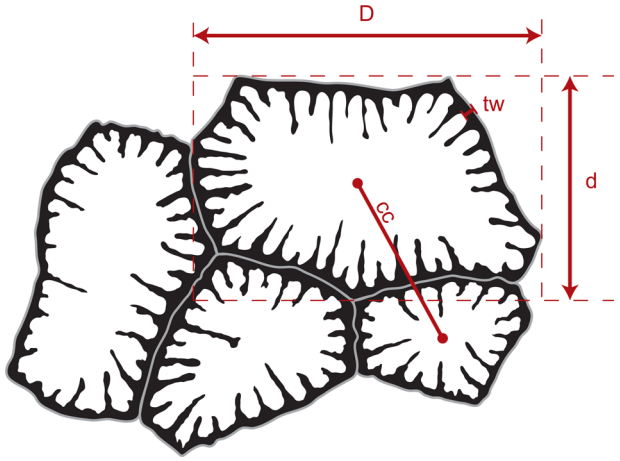

Fig. 2. Illustration of the main values measured for the morphometric study of corals. The black area corresponds to the skeleton. D calicular great diameter, d calicular small diameter, tw thickness of the wall, cc distance from corallite to corallite.

* with the publication of this work, the species can be regarded as available under the terms of Article 11 of the International Code of Zoological Nomenclature (1999).

we accept the responsibility of linking the species to this reference.

(no sign) we have no reason to doubt the attachment of the species to this reference.

? we consider the allocation of this reference must be subject to some doubt.

non we do not attach the species to this reference.

v for "Vidimus", means that we have checked the deposited specimens that relate to the cited work.

p the reference is only partially applicable to the species under discussion.

Year in italics the species is mentioned without description or illustration.

All the species are described below and presented in systematic order. A summary is available in Table 3 with the number of specimens per location and the colonial arrangement of each genus. The specimens reported in synonymies concerning (Boivin, 2019) are the same specimens described and illustrated here.

3.1 Abbreviations of institutions used

BRLSI Bath Royal Literary and Scientific Institution, United Kingdom.

BSPG Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany.

DGR Direction de la Géologie, Ministère de l'Energie, des Mines et du Développement Durable – Département de l'Energie et des Mines, Rabbat, Morocco.

MHNG Muséum d'Histoire Naturelle of Geneva, Switzerland.

MNHN Muséum National d'Histoire Naturelle, Paris, France.

MSNP Museo di Storia Naturale dell'Università di Pisa, Calci, Italia.

Order **Hexanthiniaria?** Montanaro Gallitelli (1975)

Family **Hispaniastraeidae** (Boivin, Vasseur and Lathuilière (2019)

Genus ***Hispaniastraea*** Turnšek and Geyer (1975)

Type species. *Hispaniastraea murciana* Turnšek and Geyer (1975) by original designation.

Originally included species. *Hispaniastraea murciana* (Turnšek and Geyer, 1975) and *Hispaniastraea ramosa* (Turnšek and Geyer, 1975).

Etymology. *Hispania* from Spain in Latin.

Similarities and differences. The genus *Hispaniastraea* can be confused with the hypercalicified sponge genus *Pseudoseptifer* (Fischer, 1970) due to the similarities of their skeletons. A set of ten morphological features to distinguish these taxa is presented in Boivin *et al.* (2019).

Status. Available and valid

Hispaniastraea murciana Turnšek and Geyer (1975)
Figures 3 and 4

* 1975 *Hispaniastraea murciana* sp. nov. — Turnšek & Geyer *in* Turnšek *et al.*, p. 138, Pl. 20 figs. 1–2, Pl. 21 figs. 1–2.

1975 *Hispaniastraea ramosa* sp. nov. — Turnšek & Geyer *in* Turnšek *et al.*, p. 139, Pl. 22 figs. 1–3.

? 1980 *Chaetetes* (*Pseudoseptifer*) *murciana* (Turnšek & Geyer) — Beauvais, p. 30, Pl. 3 fig 2.

v. 1980 *Blastochaetetes dresnayi* sp. nov. — Beauvais, p. 33–35, figs. 6–7, Pl. IV fig. 2.

? 1991 *Hispaniastraea ramosa* Turnšek & Geyer — Prinz, p. 167, Pl. 2 fig. 5.

? 1994 *Hispaniastraea ramosa* Turnšek & Geyer — Senowbari-Daryan & Stanley, p. 52–53, fig. 5, Pl. 1 figs. 4–8.

? 2003 *Hispaniastraea ramosa* Turnšek & Geyer — Turnšek *et al.*, p. 292–293, Pl. 3 figs. 1–4.

v. 2018 *Hispaniastraea murciana* Turnšek & Geyer — Vasseur, p. 216–217, fig. 3 .46.

v. 2019 *Hispaniastraea murciana* Turnšek & Geyer — Boivin *etal.*, p. 8–10, figs. 4–5.

v. 2019 *Hispaniastraea murciana* Turnšek & Geyer — Boivin, p. 212, figs. 10.14 and 10.15.

v. 2021 *Hispaniastraea murciana* — Vasseur and Lathuilière, p. 1231, fig. 29.

Type designation. Holotype by original designation, col. no. 33, Turnšek *et al.* (1975), p. 138.

Type locality and horizon. Upper Sinemurian – lower Pliensbachian from Zarcilla de Ramos, Province of Murcia, Spain.

Originally included material. Three colonies (33a, 33b and 34) and two fragments of colonies (35 and 36) from the same horizon as the holotype of the Seyfried collection, reposited at the Departamento de Paleontología of the University of Granada (UG), Spain.

Etymology. *murciana* from province of Murcia (Spain).

Material examined. 17 specimens: SB–53/1, SB–54, SB–55/4, SB–64/4, SB–85, SB–141, SB–145/2, SB–161/2, SB–163, SB–169/3, SB–233, SB–243, SB–246, SB–247, SB–315, SB–336 and SB–346/2.

Ages and localities of material. Upper Sinemurian from Serdrar reef, upper Sinemurian or lowermost Pliensbachian from Castle olistolith and lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Table 3. List of genera and species with their distribution by localities and colonial structures. The numbers correspond to the numbers of specimens and brackets to doubtful assignations.

Taxa	Dromedary	Serdrar	Castle	Owl	Total	Cerioid	Meandroid	Phaceloid	Plocoid	Ramose	Solitary	Thamnasterioid
Order HEXANTHINIARIA ? (Montanaro Gallitelli, 1975)												
Family Hispaniastraeidae (Boivin, Vasseur & Lathuilière, 2019)												
Genus *Hispaniastraea* (Turnšek & Geyer, 1975)						X				X		
Hispaniastraea murciana (Turnšek & Geyer, 1975)		6	7	4	17							
Order SCLERACTINIA (Bourne, 1900)												
Family Actinastreidae (Alloiteau, 1952)												
Genus *Chondrocoenia* (Roniewicz, 1989)						X			X	X		
Chondrocoenia clavellata (Terquem & Piette, 1865)	1	2			3							
Chondrocoenia martini (Fromentel, 1860)			1	1	2							
Genus *Lochmaeosmilia* (Wells, 1943)								X				
Lochmaeosmilia? sp.			(1)		(1)							
Family Astraeomorphidae (Frech, 1890)												
Genus *Parastraeomorpha* (Roniewicz, 1989)												X
Parastraeomorpha minuscula (Roniewicz, 1989)				1	1							
Family Comoseriidae (Fromentel, 1861)												
Genus *Eocomoseris* (Melnikova, Roniewicz & Löser, 1993)										X		X
Eocomoseris minima (Beauvais, 1986)		9	6	1	16							
Family Conophylliidae (Alloiteau, 1952)												
Genus *Araiophyllum* (Cuif, 1975)								X				
Araiophyllum triasicum (Cuif, 1975)				1	1							
Genus *Thecactinastraea* (Beauvais, 1986)								X				
Thecactinastraea fasciculata (Beauvais, 1986)			2		2							
Thecactinastraea termierorum (Beauvais, 1986)		4			4							
Family Cuifiidae (Melnikova, 1975)												
Genus *Coryphyllia* (Cuif, 1975)											X	
Coryphyllia capillaria (Vasseur & Lathuilière 2021)		4		3 (+1)	7 (+1)							
Coryphyllia regularis (Cuif, 1975)			3 (+1)	2 (+2)	5 (+3)							
Coryphyllia subregularis (Beauvais, 1986)			(1)		(1)							
Genus *Paracuifia* (Melnikova, 2001)								X				
Paracuifia castellum n. sp.			1		1							
Family Dermosmiliidae (Koby, 1889)												
Genus *Proleptophyllia* (Alloiteau, 1952)											X	
Proleptophyllia granulum (Fromentel & Ferry, 1866)		(1)	1	1	2 (+1)							
Family Latomeandridae (Alloiteau, 1952)												
Genus *Periseris* (Ferry, 1870)												X
Periseris elegantula (Orbigny, 1850)				2	2							
Family Protoheterastraeidae (Cuif, 1977)												
Genus *Paravolzeia* (Roniewicz *et al.*, 2005)								X				
Paravolzeia? *alpina*? (Roniewicz *et al.*, 2005)		(1)			(1)							
Family Reimaniphylliidae (Melnikova, 1975b)												
Genus *Distichophyllia* (Cuif, 1975)											X	
Distichophyllia norica (Frech, 1890)		3 (+1)	2 (+2)		5 (+3)							

Table 3. (continued).

Taxa	Dromedary	Serdrar	Castle	Owl	Total	Cerioid	Meandroid	Phaceloid	Plocoid	Ramose	Solitary	Thamnasterioid
Genus *Retiophyllia* (Cuif, 1966)								X				
Retiophyllia? *cf. gracilis* (Roniewicz, 1989)		(1)			(1)							
Family Stylophyllidae (Frech, 1890)												
Genus *Epismiliopsis* (Alloiteau, 1952)											X	
Epismiliopsis sp.		1			1							
Genus *Lepidophyllia* (Duncan, 1868)						X						
Sub-genus *Heterastraea* (Tomes, 1888)												
Lepidophyllia (*Heterastraea*) *microcalix* n. sp.	1	27	1	2	31							
Genus *Phacelostylophyllum* (Melnikova, 1972)								X				
Phacelostylophyllum martini (Fromentel, 1860)		2			2							
Phacelostylophyllum suttonensis (Duncan, 1867)	(1)		1 (+2)		1 (+3)							
Genus *Pinacophyllum* (Frech, 1890)								X				
Pinacophyllum sp.		(1)	(1)		(2)							
Genus *Stylophyllopsis* (Frech, 1890)								X				
Stylophyllopsis cf. walliae (Duncan, 1867)		1			1							
Family Thecosmiliidae (Duncan, 1884)												
Genus *Vallimeandropsis* (Beauvais, 1966)							X					
Vallimeandropsis davidsoni (Edwards and Haime, 1851a)		1	2		3							
Family Incertae sedis												
Gen. indet.						X						
Gen. indet. sp.		1			1							
Genus *Neorylstonia* (Vasseur *et al.*, 2019)											X	
Neorylstonia pseudocolumellata (Beauvais, 1986)		2	2	1 (+1)	5 (+1)							

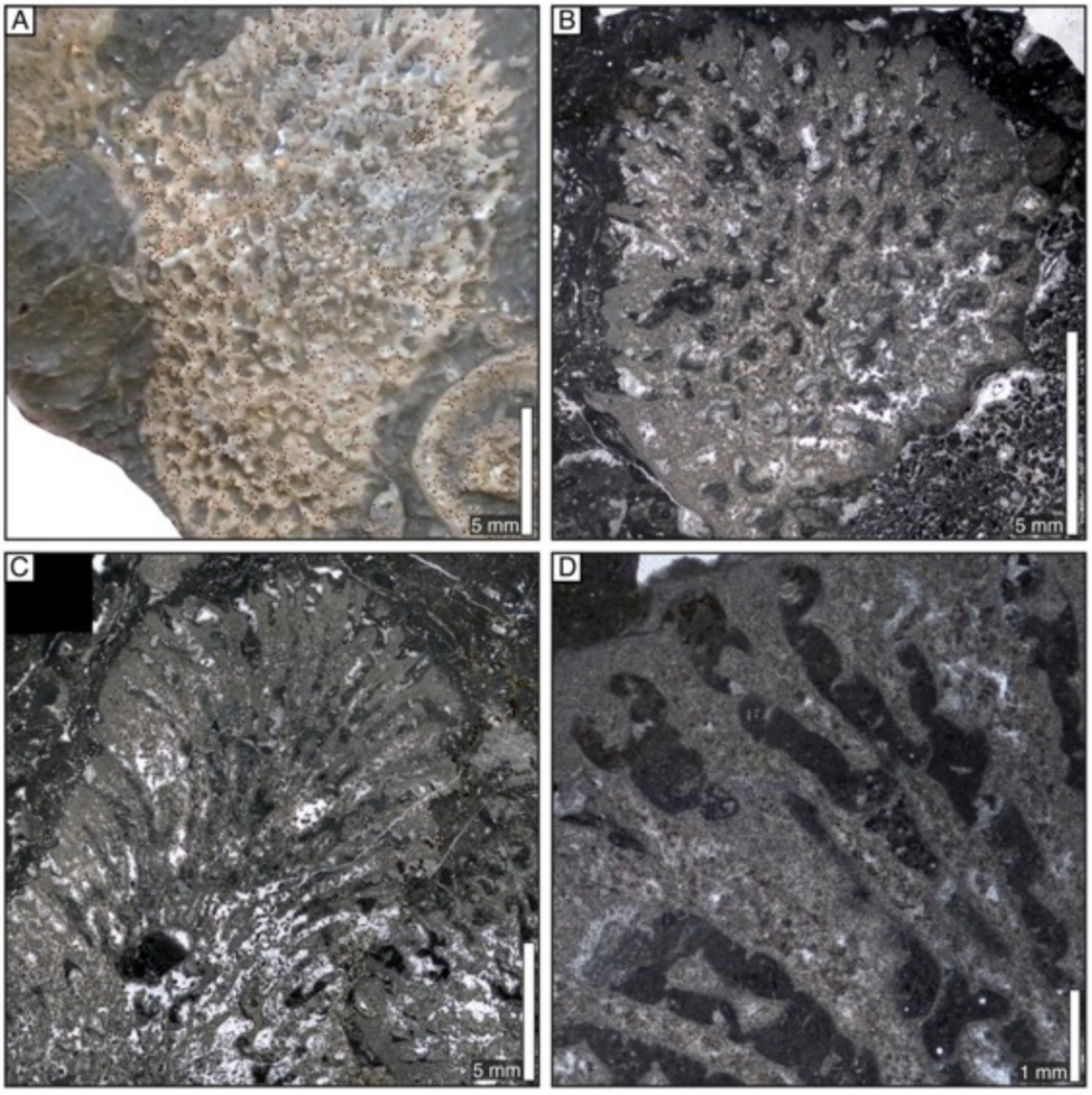

Fig. 3. *Hispaniastraea murciana* Turnšek *et al.* (1975). A Natural transverse section of the specimen SB–243. B Transverse thin section of a branch of the specimen SB–246. C–D Longitudinal thin sections of branches of the specimen SB–246.

Description. Colonies massive in shape or ramose, cerioid. Transverse section of corallites is sub-circular or polygonal. Septal apparatus characterized by one major septum highly dominant in length and thickness, and up to eleven minor septa. The major septum is straight or sometimes curved, compact, without ornamentation apart from the auriculae on the inner margin of the septum and reaches the centre of the lumen. Inner margin of the major septum is enlarged at the level of the auriculae and rounded otherwise, the lumen is typically horseshoe-shaped. Minor septa are very short, often not discernible on the surface of the inner wall, compact, and their outline in transverse section varies from triangular to semi-circular. Inner margins of the minor septa with sharp granules that alternate in height with the auriculae of the major septum. Corallites could be connected by canals. Endotheca made of thin tabulae rarely preserved.

Dimensions. Calicular great diameter 0.45 to 1.38 mm — Calicular small diameter 0.14 to 1 mm — Diameter of branches 10 to 15.78 mm — Distance from corallite to corallite 0.5 to 2.1 mm — Thickness of the wall 0.09 to 0.84 mm — Width of major septum (at its middle) 51 to 574 μm — Length of major septum 100 to 600 μm — Number of visible septa 1 to 12 septa.

Similarities and differences. *Hispaniastraea murciana* (Turnšek and Geyer, 1975) differs from *Hispaniastraea ousriorum* (Boivin, Vasseur and Lathuilière, 2019) that shows one to four well-developed S1 septa in addition to the major septum.

Stratigraphic and geographic distribution. Sinemurian – lower Toarcian from Murcia (Spain), Middle and High Moroccan Atlas Mountains (Morocco), Languedoc (France), Calabria (Italia), as well as possibly North Chile and Peru, if the identifications of Prinz (1991) and Senowbari-Daryan and Stanley (1994) are confirmed.

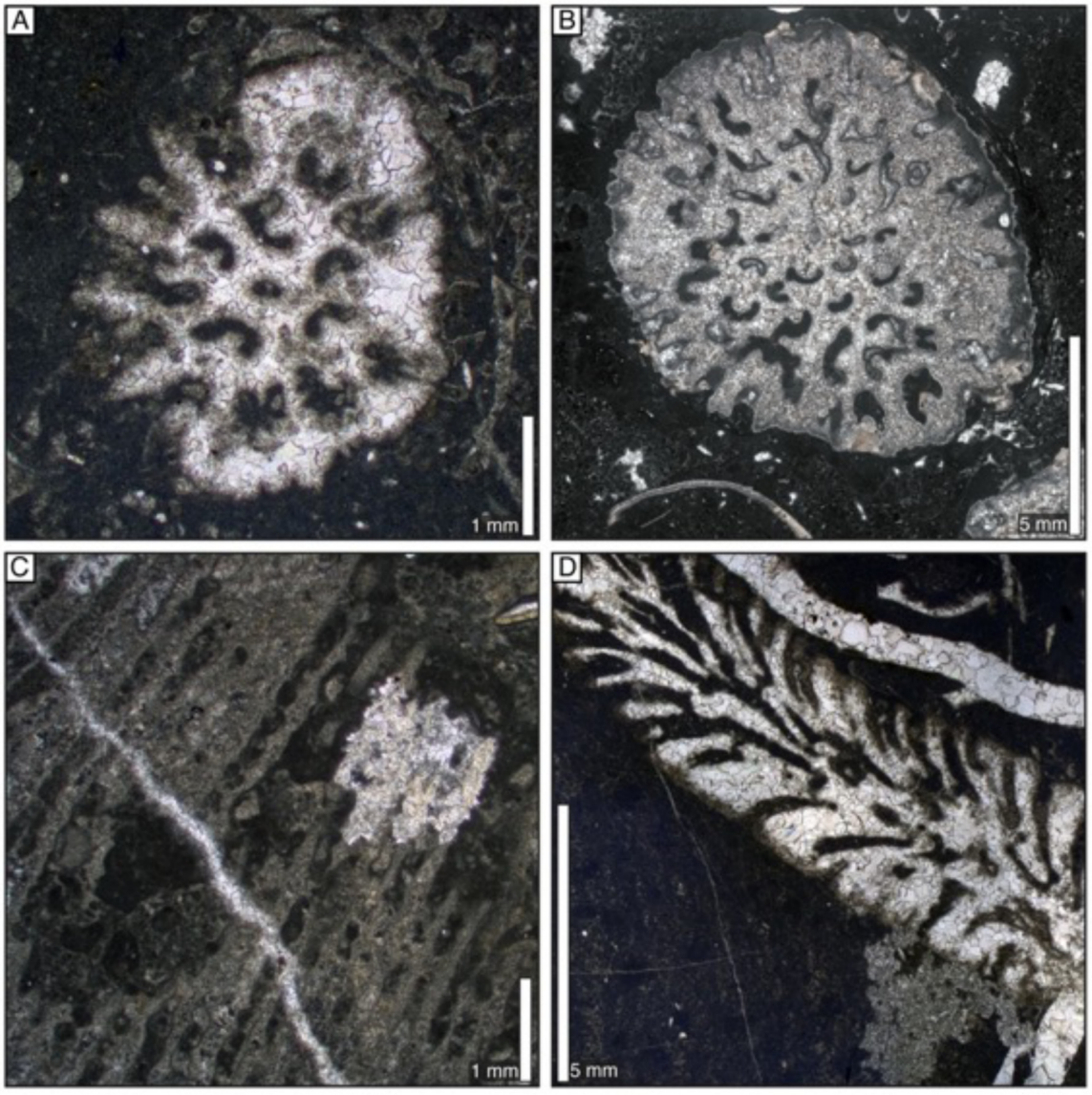

Fig. 4. *Hispaniastraea murciana* Turnšek *et al.* (1975). A Transverse thin section of a branch of the specimen SB–54. B Transverse thin section a branch of the specimen SB–85. C Longitudinal thin section of the specimen SB–169. D Longitudinal thin section of a branch of the specimen SB–53.

Order **Scleractinia** (Bourne, 1900)

Family **Actinastreidae** (Alloiteau, 1952)

Genus ***Chondrocoenia*** (Roniewicz, 1989)

Type species. *Prionastraea schafhaeutli* (Winkler, 1861) by original designation.

Originally included species. *Chondrocoenia schafhaeutli* (Winkler, 1861), *Chondrocoenia waltheri* (Frech, 1890), *Chondrocoenia ohmanni* (Frech, 1890), *Chondrocoenia* sp. A and *Chondrocoenia* sp. B.

Similarities and differences. The genus *Chondrocoenia* differs from other Actinastreidae genera by its peritheca.

Etymology. *Chondros* a grain shaped object and *koinos* common from the granulated appearance of the coenosteum surface, both in ancient Greek.

Status. Available and valid.

Chondrocoenia clavellata (Terquem and Piette, 1865)

Figure 5

* 1865 *Astrocoenia clavellata* sp. nov. — Terquem & Piette, p. 130–131, Pl. 18 fig. 4–5.

1936 *Astrocoenia clavellata* Terquem & Piette — Joly, p. 172.

v. 2014 *Chondrocoenia clavellata* (Terquem & Piette) — Gretz, p. 99–102, Pl. 7–8.

v. 2018 *Chondrocoenia clavellata* (Terquem & Piette) — Boivin *etal.*, fig. 3–c-d.

v. 2019 *Chondrocoenia clavellata* (Terquem & Piette) — Boivin, p. 188-189, fig. 10.2.

Type designation. Syntypes, no lectotype designated.

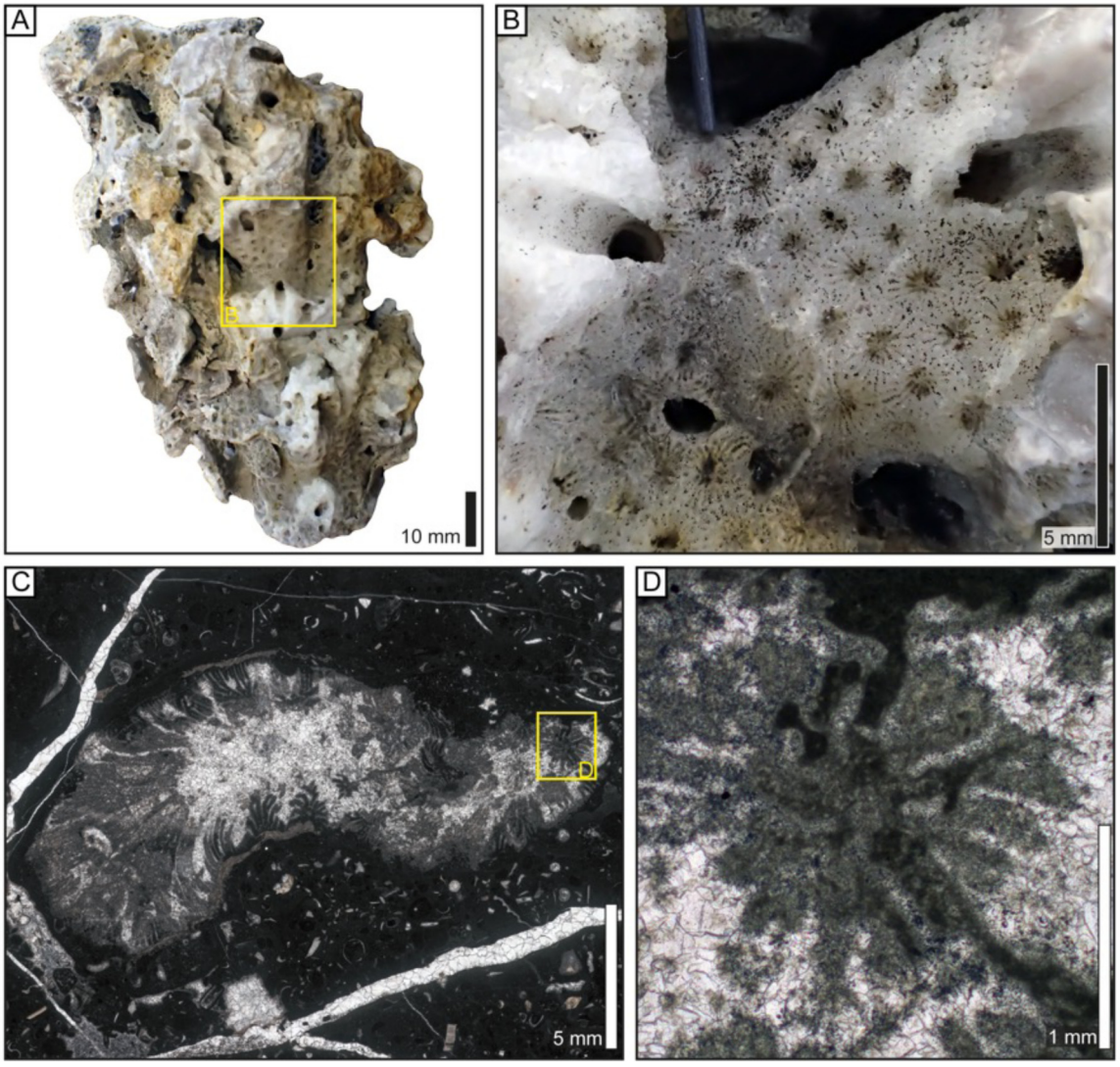

Fig. 5. *Chondrocoenia clavellata* (Terquem and Piette, 1865). A Specimen SB–194. B Enlargement of A. C Longitudinal thin section of branch of the specimen SB–49. D Enlargement of C.

Type locality and horizon. Upper Hettangian – lower Sinemurian from Laval-Morency, Chilly, Maubert-Fontaine, Charleville and Saul, Northeastern France.

Originally included material. Unspecified. We did not localise the housing institution.

Etymology. From *clava:* club in Latin referring to the shape of branches.

Material examined. 3 specimens: SB–49, SB–194 and SB–318/2.

Ages and localities of material. Sinemurian from Dromedary biostrome and upper Sinemurian from Serdrar reef, Amellagou Region, High Atlas Mountains, Morocco.

Description. Ramose colonies, cerioid to plocoid. Transverse section of corallites sub-circular or polygonal. Radial elements are costosepta. Septa are thin, straight or curved, free or sometimes joined, confluent or sub-confluent, sub-compact. Septal apparatus ordered in two size orders. Lateral faces of septa are granulated. Inner margin of septa is rounded or slightly enlarged. Trabecular projections in the axial region. Columella styliform. Peritheca made of costae, dense, with granulated aspect in distal view of natural surface. Corallites inside branches are distributed in water-jet.

Dimensions. Calicular diameter 1 to 2 mm — Distance from corallite to corallite circa 0.9 to 1.7 mm — Septal density 6 to 8 septa per 1 mm.

Similarities and differences. See *Chondrocenia martini* below.

Stratigraphic and geographic distribution. Hettangian – Sinemurian from France, Belgium and Morocco (High Atlas Mountains).

Chondrocoenia martini (Fromentel, 1860)
Figure 6

*v 1860 *Stylastraea martini* sp. nov. — Fromentel *in* Martin, p. 94, Pl. 7 fig. 18-19.

1861 *Stylastraea martini* Fromentel — Fromentel, p. 223.

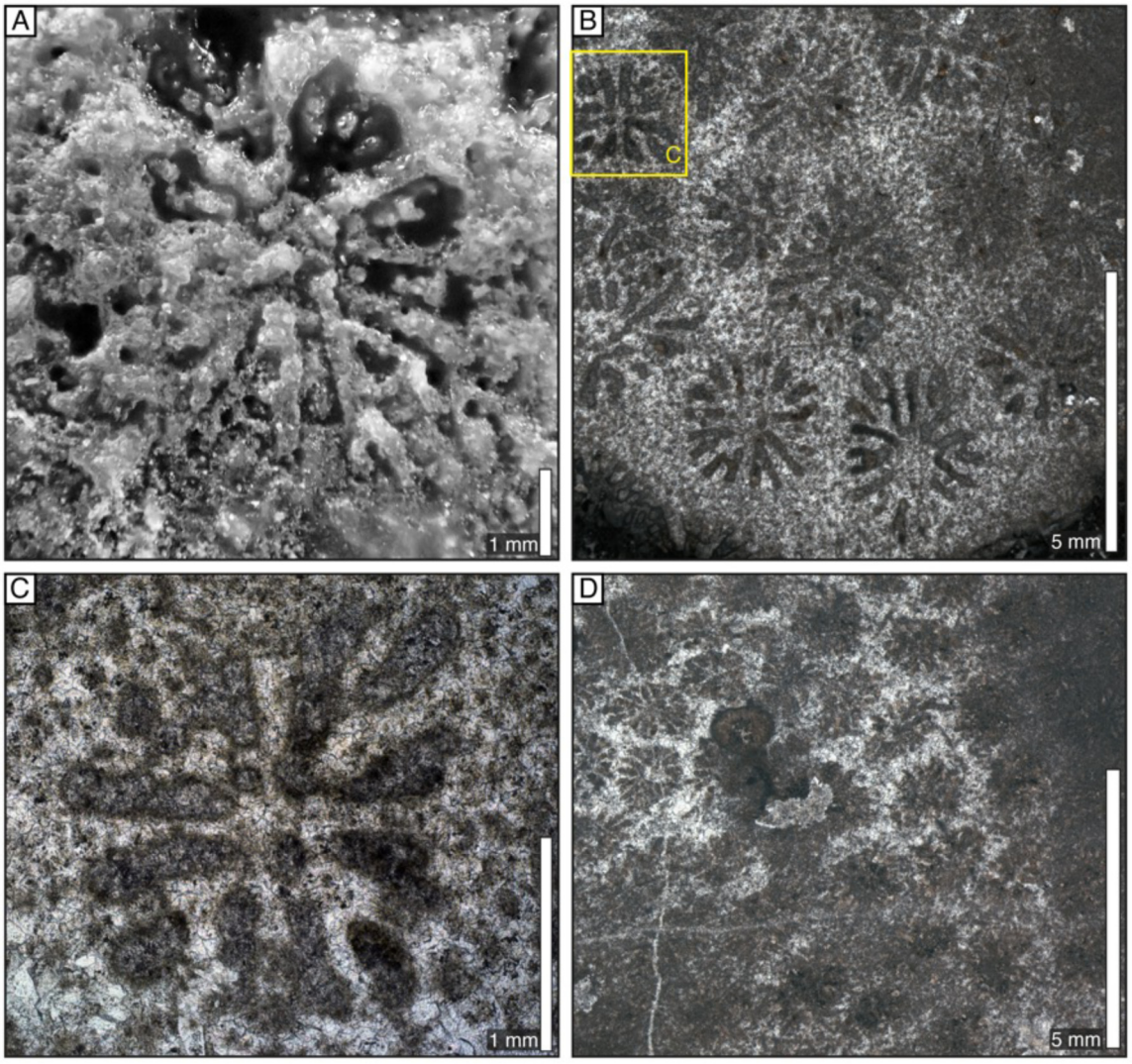

Fig. 6. *Chondrocoenia martini* (Fromentel, 1860). A Natural view of a calice of the specimen SB–343. B Transverse thin section of the specimen SB–343. C Enlargement of B. D Transverse thin section of the specimen SB–157.

1865 *Stylastraea martini* Fromentel — Terquem & Piette, p. 167.

1867 *Astrocoenia plana* sp. nov. — Duncan, p. 19, Pl. 5 fig. 1.

1867 *Astrocoenia reptans* sp. nov. — Duncan, p. 20, Pl. 4 figs. 4–5 and 15.

1867 *Astrocoenia superba* sp. nov. — Duncan, p. 21, Pl. 9 figs. 3–4.

1867 *Cyathocoenia costata* sp. nov. — Duncan, p. 29, Pl. 5 figs. 10–11.

1884b *Stylastraea martini* Fromentel — Tomes, p. 370.

1912 *Stylastraea martini* Fromentel — Lissajous, p. 179, pl. 18 fig. 54.

1917 *Astrocoenia lissoni* sp. nov. — Tilmann, p. 701, Pl. 26 fig. 4.

? 1953 *Astrocoenia* sp. *cf. lissoni* Tilmann —Wells, p. 3, fig. 1.

1976 *Actinastraea plana* (Duncan) — Beauvais, p. 44, Pl. 8 figs. 1–4, text-figs. 1–2.

1991 *Actinastrea plana* (Duncan) — Prinz, p. 161, Pl. 1 fig. 11.

1994 *Actinastraea plana* (Duncan) — Stanley & Beauvais, p. 43.

2013 *Stylastraea martini* Fromentel — Lathuilière, www.corallosphere.org with figures.

v. 2019 *Chondrocoenia plana* (Duncan) — Boivin, p. 190-191, fig. 10.3.

Type designation. Syntype. MHNG GEPI 036087.

Type locality and horizon. Hettangian (initially described in the *Ammonites moreanus* zone), from Vic de Chassenay, Côte d'Or, France.

Originally included material. Unspecified.

Etymology. Dedicated to Jules Martin.

Material examined. 2 specimens: SB–157 and SB–243.

Ages and localities of material. Upper Sinemurian or lowermost Pliensbachian from Castle olistolith and lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

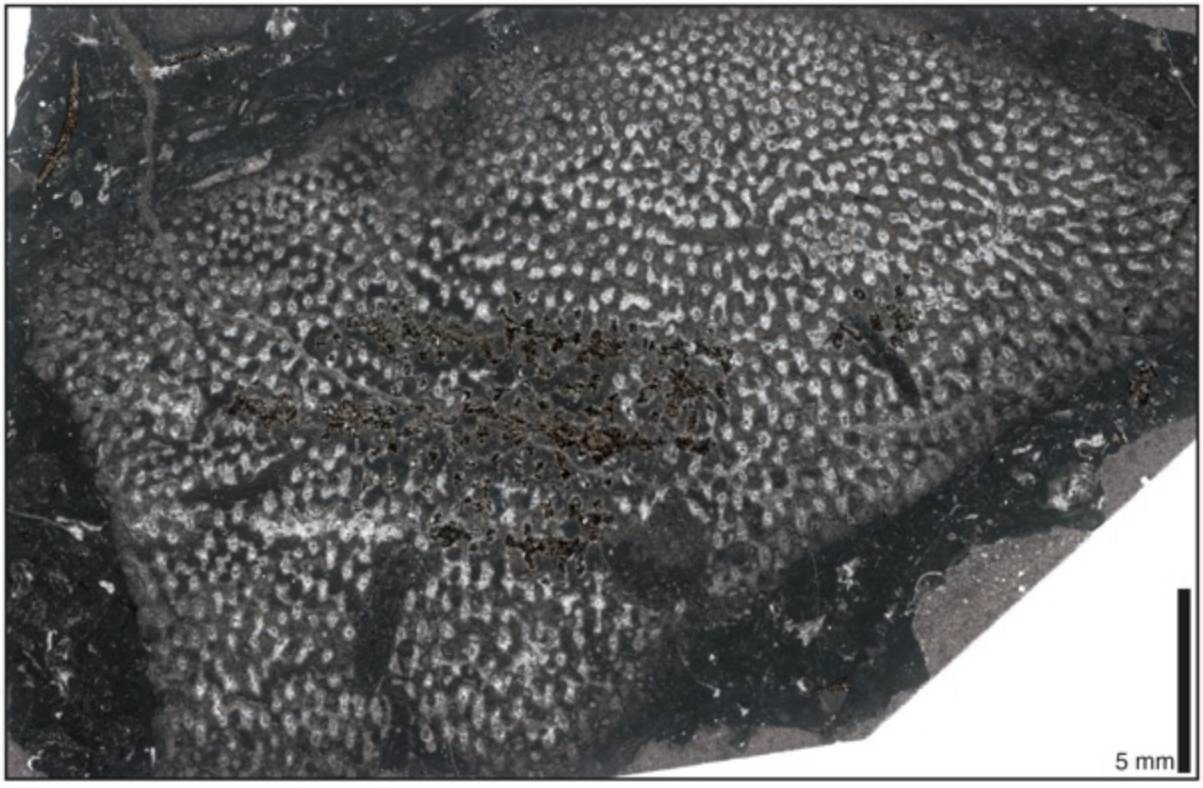

Fig. 7. *Lochmaeosmilia*? sp. Transverse thin section of the specimen SB–155.

Table 4. Comparison of dimensions between species of *Lochmaeosmilia* and *Apocladophyllia*.

Species	Diameter of corallite	Number of septa
Lochmaeosmilia aethiopica (Wells, 1943)	0.6 to 1 mm	10
Lochmaeosmilia besavoensis (Alloiteau, 1958)	1.5 to 3 mm	18 to 46
Lochmaeosmilia nodosa (Alloiteau, 1958)	1.8 to 2.5 mm	28 to 50
Lochmaeosmilia radiata (Lamouroux, 1821)	1 mm	12
Lochmaeosmilia trapeziformis (Gregory, 1900)	0.8 to 2 mm	4 to 17
Apocladophyllia? *gozdensis* (Turnšek *et al.*, 2003)	1.8 to 2.3 mm	30 to 35
Apocladophyllia guigouensis (Vasseur, 2018)	2 to 3.3 mm	28 to 31
Apocladophyllia koniakensis (Ogilvie, 1897)		
including *A. chaputi* (Alloiteau, 1939)	1.8 to 2 mm	12 to 24
Apocladophyllia nowaki (Morycowa & Roniewicz, 1990)	2.7 to 3.8 mm	48

Description. Colonies cerioid to plocoid. Massive in shape. Transverse section of corallite circular to sub-circular. Septa are thick, straight, free or joined, compact, non-confluent. Septal apparatus organized in two size orders, typically eight to twelve S1 and a variable number of S2. S2 septa are thinner than S1 septa. Septal junctions are very regular: S2 septa are joined to neighbouring S1 septa. Lateral faces of S1 and S2 septa are ornamented with granules. Septa are enlarged at outer margin that give to corallite a multi-lobed aspect. Columella styliform. Extra-calicular budding. Radial symmetry very marked in smaller corallites. Endotheca made of dissepiments.

Dimensions. Calicular diameter 0.9 to 3.45 mm — Distance from corallite to corallite 2 to 3 mm — Septal density 3 to 4 septa per 1 mm — Number of septa circa 20 septa.

Similarities and differences. This species is close from *Chondrocoenia clavellata* (Terquem and Piette, 1865) but differs by its lower septal density and the colonial form.

Stratigraphic and geographic distribution. Hettangian from Chile and Great Britain, Sinemurian from Canada, Sinemurian – Pliensbachian from Morocco (High Atlas Mountains), Middle Liassic of Peru.

Genus ***Lochmaeosmilia*** (Wells, 1943)

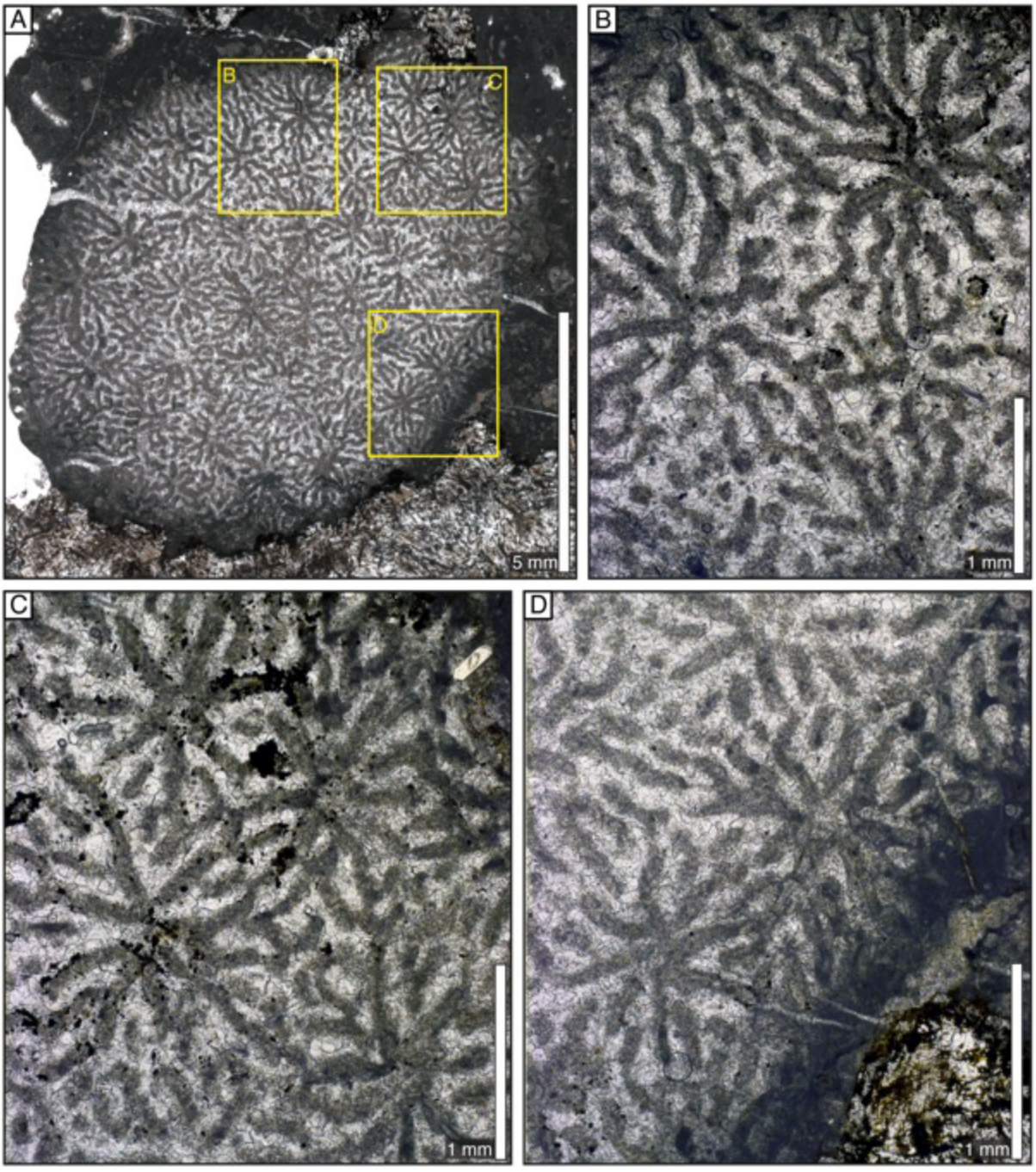

Fig. 8. *Parastraeomorpha minuscula* (Roniewicz, 1989). A Transverse thin section of the specimen SB–344. B–C–D Enlargement of A.

Type species. *Stylosmilia trapeziformis* (Gregory, 1900) by original designation.

Originally included species. *Lochmaeosmilia aethiopica* (Wells, 1943), *Lochmaeosmilia koniakensis* (Ogilvie, 1897) and *Lochmaeosmilia trapeziformis* (Gregory, 1900).

Similarities and differences. The genus *Lochmaeosmilia* is characterised by its interconnecting apophyses, a character that is known in another genus *i.e.*, *Apocladophyllia* (Morycowa and Roniewicz, 1990), a coral known in Toarcian (Vasseur *et al.*, 2021) and in the interval Kimmeridgian-Berriasian. According to Morycowa and Roniewicz (1990), the septal apparatus is regular radial and bi-radial in *Apocladophyllia*, and particularly irregular and anastomosing in *Lochmaeosmilia*. The microstructure is said to be different due to minute and dense granules in *Apocladophyllia* that have not been observed in *Lochmaeosmilia*.

Etymology. From *lochme*: thicket, copse, especially as the lair of wild beast, in ancient Greek referring to the branching form of the colony, and *smilia*: scalpel biter also in ancient Greek.

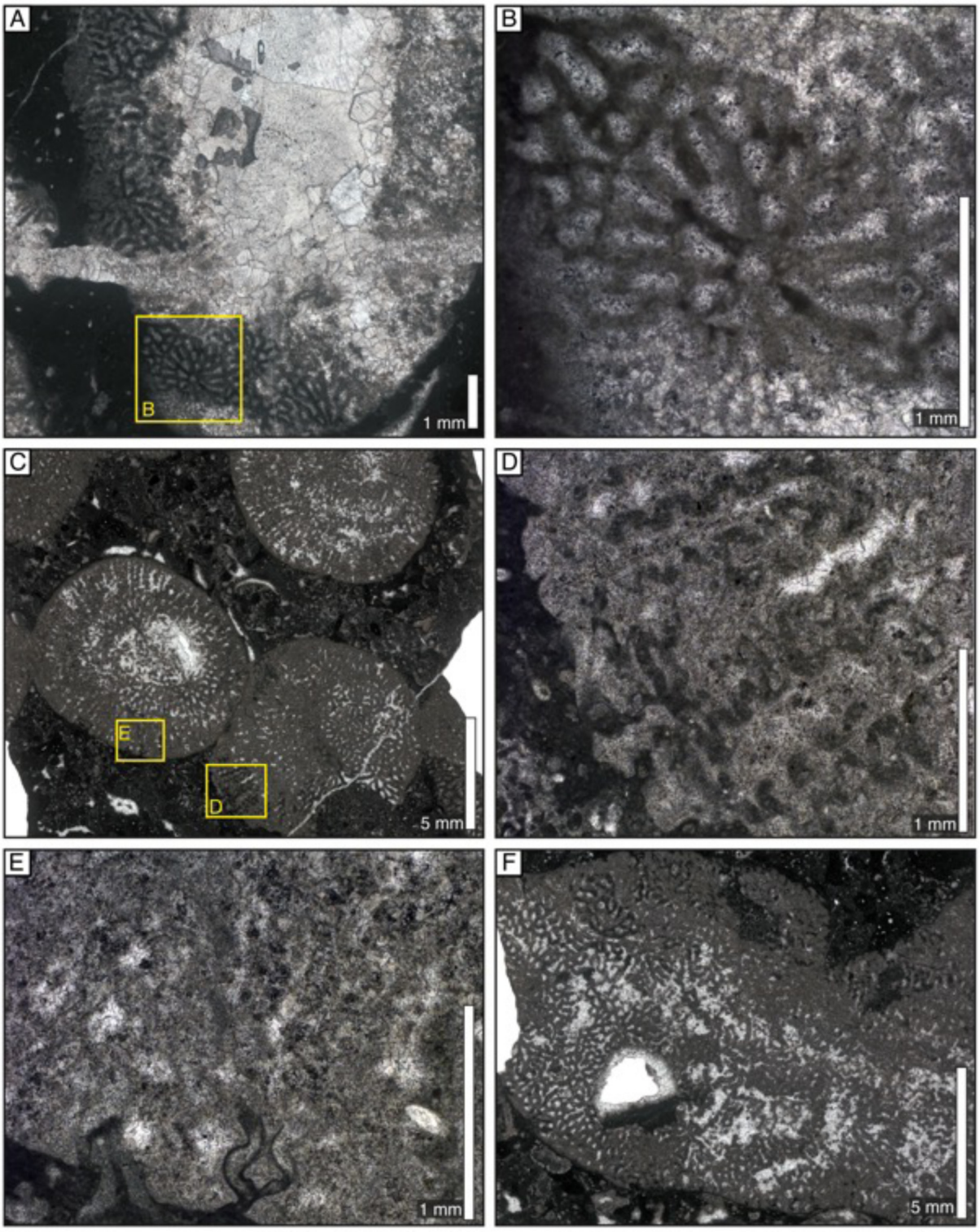

Fig. 9. *Eocomoseris minima* (Beauvais, 1986). A Longitudinal thin section of a branch of the specimen SB–222. B Enlargement of A. C Transverse thin section of branches of the specimen SB–245. D–E Enlargement of C. F Longitudinal thin sections of branches of the specimen SB–245.

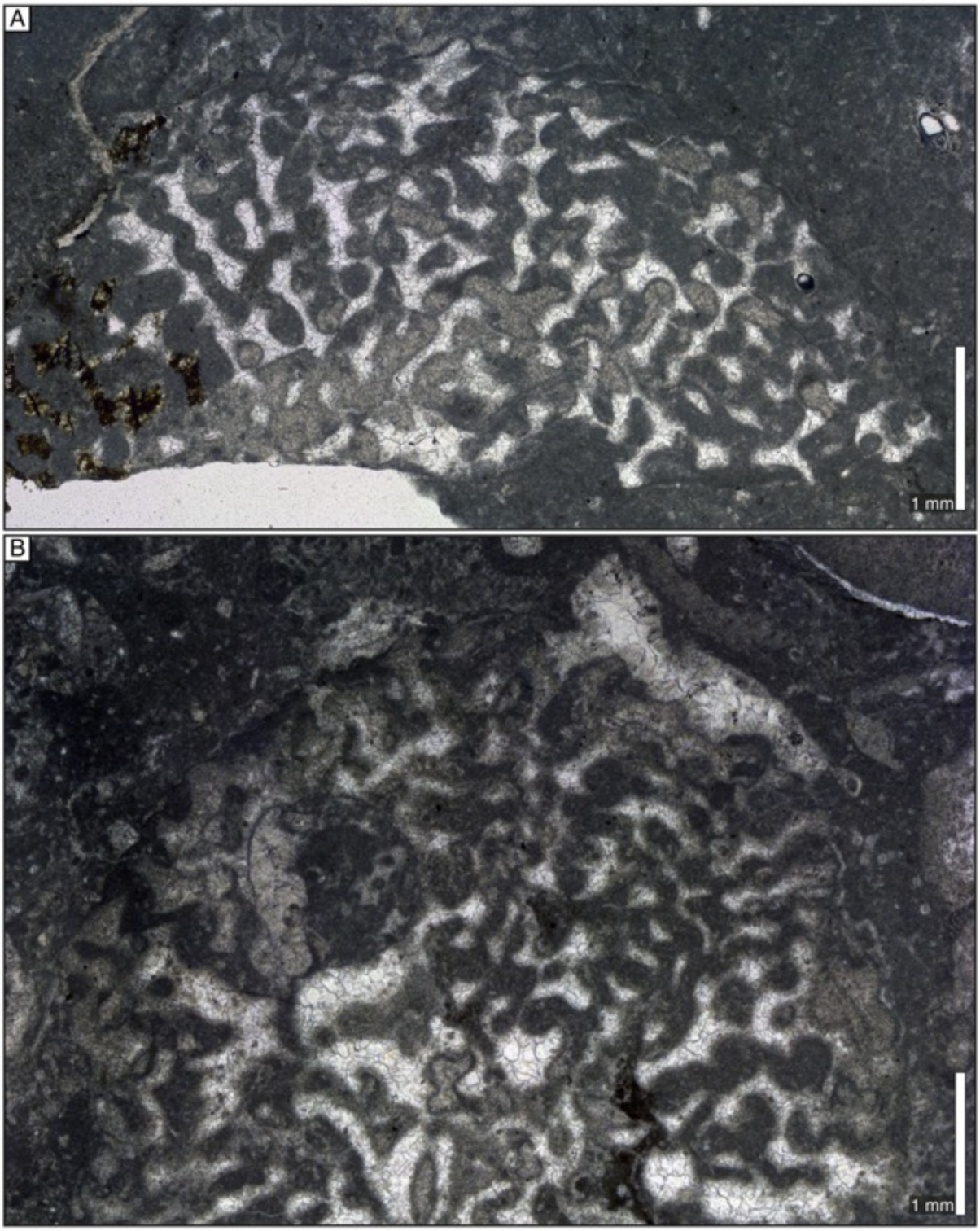

Fig. 10. *Eocomoseris minima* (Beauvais, 1986). A Longitudinal thin section of the specimen SB–167/2. B Longitudinal thin section of the specimen SB–316/2.

Fig. 11. *Araiophyllum triasicum* (Cuif, 1975b). Transverse thin section of the specimen SB–242/2.

Status. Available and valid.

***Lochmaeosmilia*? sp.**

Figure 7

Material examined. 1 colony: SB–155.

Ages and localities of material. Upper Sinemurian or lowermost Pliensbachian from Castle olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Branching colony with high density of calices, extensively recrystallised. Septal apparatus almost not visible (Fig. 7). Branches are regularly connected witch each other by apophyses.

Dimensions. Diameter of corallites 0.3 mm — 3 to 4 branches per mm^2 — Number of septa: 12 (approximated from a quarter of calix) — Septal density: 2 septa per 100 µm.

Remarks. The preservation of our single specimen does not allow a formal identification, despite it is probably a new species. The diagnostic characters of the septa were not observed, that is why we put a question mark after the genus name.

Similarities and differences. Our specimen can be distinguished from other nominal species of *Lochmaeosmilia* by the low size of its corallites (Tab. 4). This is also valid for species of *Apocladophyllia* (Tab. 4).

Stratigraphic and geographic distribution. Sinemurian – lowermost Pliensbachian from Morocco (High Atlas Mountains). The extension of the genus which was considered Middle Jurassic in age (Beauvais, 1971), is probably much wider.

Family **Astraeomorphidae** (Frech, 1890)

Genus ***Parastraeomorpha*** (Roniewicz, 1989)

Type species. *Parastraeomorpha minuscula* (Roniewicz, 1989) by original designation.

Originally included species. *P. minuscula* (Roniewicz, 1989) and *P. similis* (Roniewicz, 1989).

Similarities and differences. This genus is close to *Astraeomorpha* (Reuss, 1854) but differs by the lack of menianae and the development of thick synapticulae with oblique axes whereas they are horizontal in *Parastraeomorpha*.

Etymology. From *para*: near in ancient Greek, referring to the morphological similarity to *Astraeomorpha* (Reuss, 1854).

Status. Available and valid.

Parastraeomorpha minuscula (Roniewicz, 1989)

Figure 8

p 1890 *Astraeomorpha confusa* Winkler. var. nov. *minor* — Frech, p. 68, Pl. 19 figs. 4, 11 and 12 (non fig. 1, nec 7).

* 1989 *Parastraeomorpha minuscula* sp. nov. — Roniewicz, p. 98-99, Pl. 30 figs. 1–2.

2003 Parastraeomorpha minuscula Roniewicz — Stanley & Yarnell, p.114.

v. 2019 *Parastraeomorpha minuscula* Roniewicz — Boivin, p. 230-231, fig. 10.22.

Type designation. Holotype by original designation, NHMW 1982/57/17, (Roniewicz, 1989): p.98, Pl. 30 fig. 1.

Type locality and horizon. Rhaetian from Zlambach Beds of Fischerwiese, Northern Calcareous Alps, Austria.

Originally included material. Twenty-five fragments of colonies and four thin-sections.

Etymology. From *minuscula*: small in Latin referring to the small corallite dimensions.

Material examined. 1 colony: SB–344.

Ages and localities of material. Lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Colony thamnasterioid with some aphroid tendencies, columnar. Corallites densely distributed without apparent organisation. Radial elements are bisepta or septa, confluent or not confluent, compact, often joined, flexuous. Septal apparatus hierarchized in two size orders. S1 septa are long and reach the columella, whereas S2 septa are joined to neighbouring S1 septa. Lateral faces of septa are ornamented with probable pennulae (the only available sections are not favourable for this observation). Symmetry hexameral well

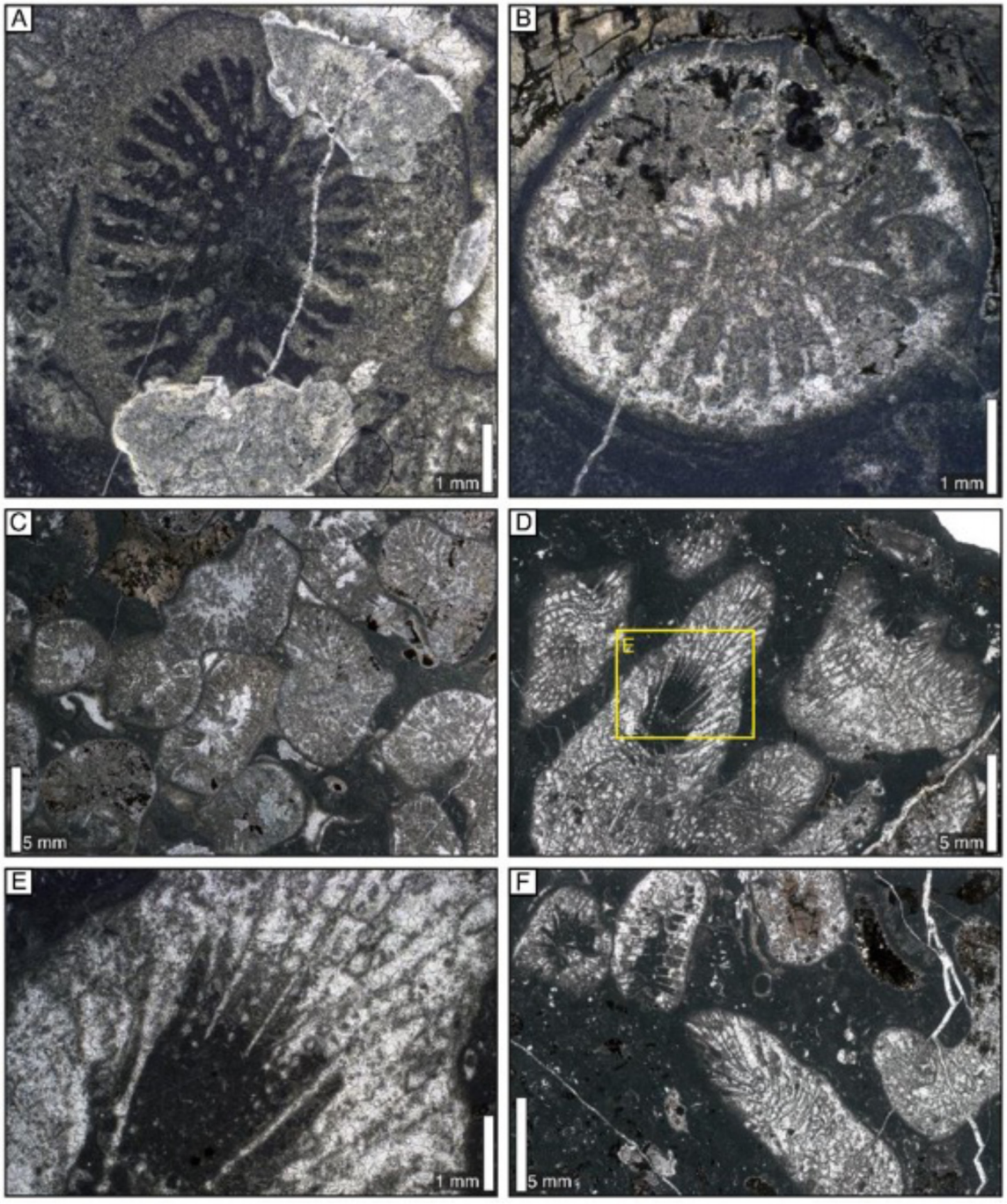

Fig. 12. *Thecactinastraea fasciculata* (Beauvais, 1986). A–C Transverse thin sections of the specimen SB–153. D Oblique thin section of the specimen SB–80. E Enlargement of D. F Oblique thin section of the specimen SB–80.

regular, indicating an intercalicular budding. Synapticula present. Axial area is occupied by a columella of unknown nature (perhaps parietal) and extremity of S1 septa. No wall.

Dimensions. Size of colony 9.4 × 11.3 mm — Calicular diameter circa 1 mm — Distance from corallite to corallite 0.9 to 1.2 mm — Number of septa circa 12–15 septa.

Similarities and differences. This species differs from *Parastraeomorpha similis* (Roniewicz, 1989) that has larger diameter of corallites, robust skeletal elements and a lamellar colony growth form.

Stratigraphic and geographic distribution. Rhaetian from Austria (Northern Calcareous Alps), Upper Triassic from Alaska, Pliensbachian from Morocco (High Atlas Mountains).

Family **Comoseriidae** (Fromentel, 1861) (= Microsolenidae Koby, 1889)

Genus ***Eocomoseris*** (Melnikova, Roniewicz and Löser, 1993)

Type species. *Eocomoseris gurumdyensis* nomen novum pro *Eocomoseris ramosa* Melnikova, 1993 non (Frech, 1890), p. 5, Pl. I fig. 1–3 by original designation. The type species is now considered to be junior synonym of *Eocomoseris minima* (Beauvais, 1986) by Vasseur and Lathuilière (2021, p. 1203).

Originally included species. *Eocomoseris gurumdyensis* Melnikova, 1993, *Eocomoseris lamellata* Melnikova, 1993, *Eocomoseris raueni* Loeser, 1993.

Similarities and differences. This genus seems very close to *Spongiomorpha* (Frech, 1890) that was placed among the Astraeomorphidae (Frech, 1890) (Roniewicz, 2010a). The connection between Astraeomorphidae and Comoseriidae remains a matter for future researches.

Etymology. *Eos* from dawn in ancient Greek and *Comoseris* referring to the comoseriid phylogeny.

Status. Available and valid.

Eocomoseris minima (Beauvais, 1986)

Figures 9 and 10

P 1982 *Actinastrea minima* nomen nudum — Beauvais, p. 1964, pl. 1, fig. 3.

* 1986 *Actinastrea minima* sp. nov. — Beauvais, p. 31, Pl. 2 fig. 6, Pl. 6 fig. 6.

1993 *Eocomoseris ramosa* sp. nov. — Melnikova, p. 5, pl. I fig 1–3.

? 1994 *Actinastraea minima* Beauvais — Stanley & Beauvais, p. 42, fig. 6a–c (non fig. 6d).

2011 *Eocomoseris gurumdyensis* nomen novum pro *Eocomoseris ramosa* Melnikova — Roniewicz, p. 422.

2011 *Eocomoseris ramosa* (Frech, 1890) — Roniewicz, p. 424, fig. 7F.

v. 2019 *Eocomoseris? cf. minima* (Beauvais) — Boivin, p. 202-203, fig. 10.9–10.12.

2021 *Eocomoseris gurumdyensis* Melnikova *in* Roniewicz — Melnikova & Roniewicz, Table 1.

2021 *Eocomoseris minima* (Beauvais) — Vasseur & Lathuilière, p. 1203, fig. 9.

Remarks. Beauvais (1982) described under the name *Actinastrea minima* one specimen from Canada and designated another Moroccan specimen as a holotype, subsequently described in Beauvais (1986). The Canadian specimen is explicitly referred to a nomen nudum and the name has been available since 1986 (Articles 11 and 13 of the International Code of Zoological Nomenclature). We assign our material to the species defined by the Moroccan holotype (designated in (Beauvais, 1982) and described in (Beauvais, 1986) but we have reservation about the Canadian specimen that looks like a real actinastreid.

Type designation. Holotype MNHN.F.R11620, by original designation (Beauvais 1986, *cf.* remark above).

Type locality and horizon. Domerian from Jebel Bou Dahar, High Atlas Mountains, Morocco.

Originally included material. 9 specimens from the collection Menchikoff.

Etymology. *minima* from the small diameter of corallites.

Material examined. 16 specimens: SB–53/2, SB–64/1, SB–144/1, SB–146/2, SB–169/1, SB–198, SB–219/1, SB–222, SB–235, SB–245, SB–313, SB–317, SB–323 and SB–334.

Ages and localities of material. Upper Sinemurian from Serdrar reef, upper Sinemurian or lowermost Pliensbachian from Castle olistolith, and lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Ramose colonies, branching or massive, thamnasterioid. Corallite small, vaguely delimited. Septa perforate, straight or curved, confluent. Septal apparatus organised in one size order. Septa are joined by two at their inner margin. Septa trabecular with pennulae, alternating with those of neighbouring septa. Columella styliform perhaps mono-trabecular (Fig. 9A). Synapticulae present.

Dimensions. Calicular diameter 1 to 2 mm — Diameter of branches 5 to 15 mm — Septal density 6 to 11 septa per 2 mm — Distance from corallite to corallite 1.2 to 1.8 mm — Width of pennulae circa 100 to 140 μm.

Similarities and differences. *Eocomoseris minima* differs from:

— *Eocomoseris lamellata* Melnikova, 1993 by its lamellar shape and well delimited corallites.

— *Eocomoseris raueni* Loeser, 1993 by its massive globular or flat shape and its larger corallites (Calicular diameter 2 to 3 mm and Distance from corallite to corallite 1.5 to 3.5 mm, according Melnikova *et al.*, 1993).

Stratigraphic and geographic distribution. Norian from Austria, Sinemurian from Canada? Sinemurian – Pliensbachian from Morocco, Pliensbachian from Tajikistan.

Family **Conophylliidae** (Alloiteau, 1952)

Genus ***Araiophyllum*** (Cuif, 1975b)

Type species. *Araiophyllum triasicum* (Cuif, 1975b), p. 110–115, Pl. 16, figs. 17 and 18, by monotypy.

Originally included species. Only the type species.

Similarities and differences. This genus is close to genera *Eocomoseris* (Melnikova, Roniewicz and Löser, 1993) and *Spongiomorpha* (Frech, 1890) by its perforated nature, but it differs by its phaceloid nature.

Etymology. From *araios*: porous and *phyllum*: leaf, both in ancient Greek.

Status. Available and valid.

Araiophyllum triasicum (Cuif, 1975b)

Figure 11

* 1975b *Araiophyllum triasicum* sp. nov. — Cuif, p. 110–115, p. 126, figs. 17–18, Pl. 16.

1989 *Araiophyllum cf. triasicum* Cuif — Turnšek & Buser, p. 86, Pl. 7 figs. 1–2.

1993 *Araiophyllum triasicum* Cuif — Cuif & Gautret, p. 407–408, Pl. 1 figs. 1–4.

1997 *Araiophyllum triasicum* Cuif — Turnšek, no 20.

v. 2019 *Araiophyllum triasicum* Cuif — Boivin, p. 186-187, fig. 10.1.

Type designation. Holotype by original designation (p. 115), MNHN.F.A79197.

Type locality and horizon. Carnian from Taurus Mountains, Lycia, Anatolia, Alakir Cay valley.

Originally included material. The text is ambiguous. Perhaps only one.

Etymology. From Triassic referring to the stratigraphic position of the material.

Material examined. 1 specimen: SB–242/2.

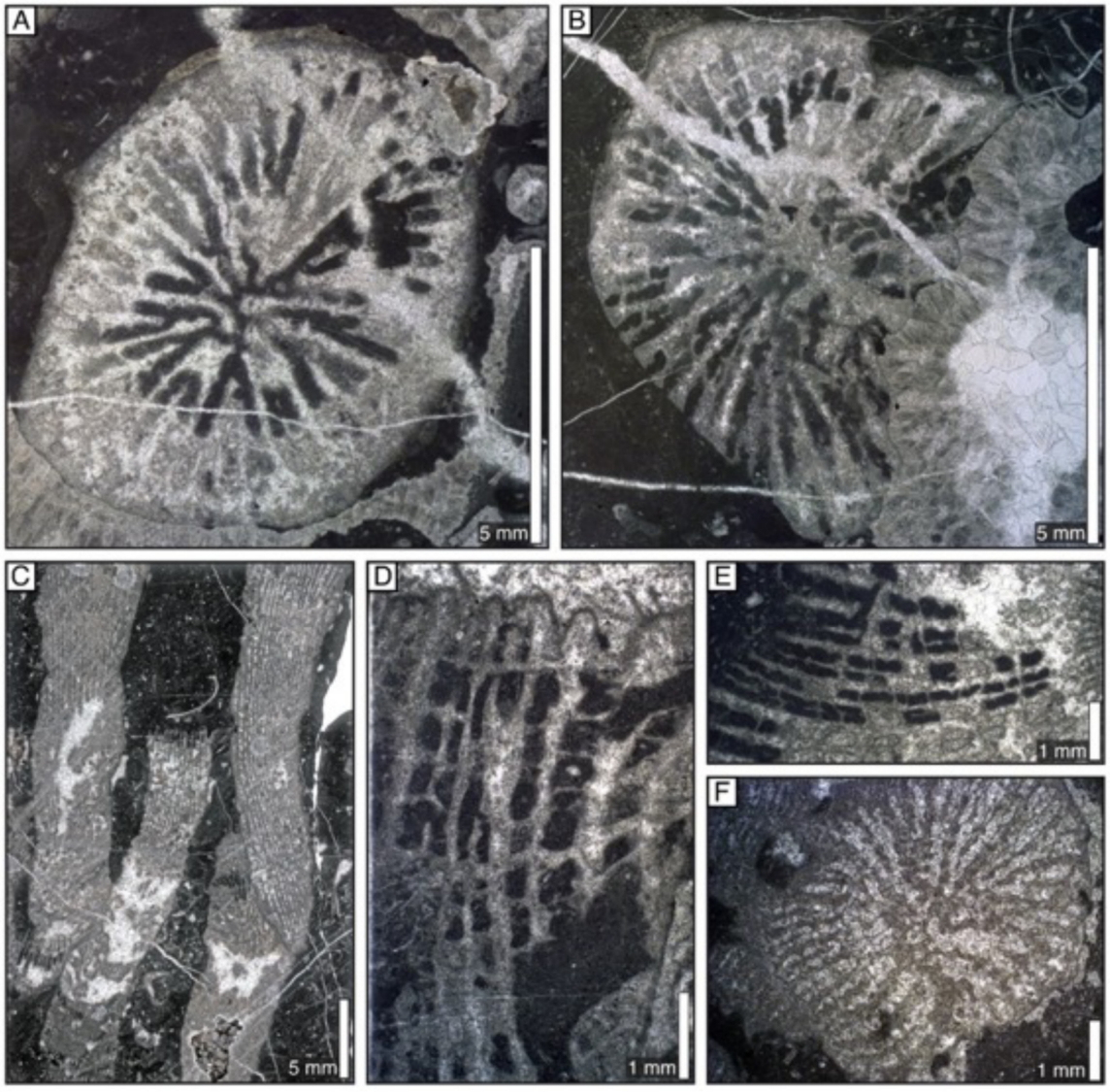

Fig. 13. *Thecactinastraea termierorum* (Beauvais, 1986). A–B Transverse thin section of the specimen SB–379. C Longitudinal thin section of the specimen SB–200. D–E Longitudinal thin section of the specimen SB–55/3. F Transverse thin section of the specimen SB–55/3.

Ages and localities of material. Lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Detached branch of a phaceloid coral. Radial elements are septa with pennulae without meniana, perforate, straight or slightly sinuous, joined. Septal apparatus organised in two size orders. S1 reach the papillose columella. S2 septa are short, sometimes contratingent on neighbouring S1 septa. Endotheca badly preserved, perhaps made of dissepiments. Perhaps pellicular epitheca.

Dimensions. Calicular great diameter 4.8 mm — Calicular small diameter 3.9 mm — Thickness of the wall circa 0.2 to 0.5 mm — Number of septa 25 or 26 septa — Septal density 3 to 4 septa per 1 mm.

Similarities and differences. *Araiophyllum triasicum* (Cuif, 1975b) differs from *Araiophyllum liassicum* (Beauvais, 1986) which has calices with a higher diameter (4 to 12 mm) and a greater septal density (12 septa per 2 mm).

Stratigraphic and geographic distribution. Carnian from Turkey (Taurus Mountains) and Slovenia (Pokljuka), Pliensbachian from Morocco (High Atlas Mountains).

Genus ***Thecactinastraea*** (Beauvais, 1986)

Type species. *Thecactinastraea fasciculata* (Beauvais, 1986) by original designation.

Originally included species. Only the type species.

Remarks. *Thecactinastraea* (Beauvais, 1986) and *Phacelophyllia* (Beauvais, 1986) are considered synonyms. In accordance with the principle of the first reviser (ICZN Art.

24.2) the priority is given to *Thecactinastraea* because the first synonymy was proposed in Melnikova and Roniewicz (2017), and not in Brame *et al.* (2019).

Similarities and differences. This genus differs from the phaceloid genera:

- *Paracuifia* (Melnikova, 2001) that has poorly ornamented septa.

- *Paravolzeia* (Roniewicz *et al.*, 2005) that has poorly ornamented septa too.

- *Phacelostylophyllum* (Melnikova, 1972) that is stylophyllid in septal structure.

- *Retiophyllia* (Cuif, 1966) that is a distichophylliid in structure and shows a typical epitheca.

Etymology. From the genera *Thecosmilia* referring to the external morphology and *Actinastraea* referring to the structure of radial elements according to (Beauvais (1986).

Status. Available and valid.

Thecactinastraea fasciculata (Beauvais, 1986)
Figure 12

* 1986 *Thecactinastraea fasciculata* sp. nov. —Beauvais, p.33, Pl. 5 fig. 1, text-fig. 21.

1986 *Myriophyllum fasciatum* sp. nov. — Beauvais, p.37, Pl. 9 fig. 1, text-fig. 25.

non 2003 *Thecactinastraea fasciculata* Beauvais — Turnšek *et al.,* p.293, Pl.4 fig. 1-5.

2003 *Phacelophyllia fasciata* (Beauvais) — Turnšek *et al.*, p.297, Pl.9 fig. 4.

2017 *Thecactinastraea fasciculata* Beauvais — Melnikova & Roniewicz, p. 133, fig. 3C, D.

v. 2018 *Phacelophyllia fasciculata* (Beauvais) — Vasseur, p. 279, fig. 3

v. 2019 *Phacelophyllia fasciculata* (Beauvais) — Boivin, p. 240, fig. 10

Remarks. *Thecactinastraea fasciculata* in Turnšek *et al.* (2003) is excluded of our synonymy because of the difference in the septal microstructure and microarchitecture similar to Cuifiidae (Melnikova, 1975b). Prinz (1991) considered *Thecosmilia suttonensis* (Duncan, 1867) to be a senior synonym of *T. fasciculata* Beauvais. We rather assign the Duncan's species to the stylophyllid genus *Phacelostylophyllum*.

Type designation. Holotype by original designation, MNHN.F.R11611.

Type locality and horizon. Lower Jurassic from Tarhilest, near of Dayet Ifrah, Morocco.

Originally included material. 4 specimens from the collection du Dresnay, no. 4975 (1 specimen) and 4569 bis (3 specimens).

Etymology. From *fasciculata*: fasciculate in Latin.

Material examined. 2 colonies: SB–80 and SB–153.

Ages and localities of material. Upper Sinemurian or lowermost Pliensbachian from Castle olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Phaceloid colonies with a high density of branches. Transverse section of corallites sub-circular or deformed by the intracalicular budding. Radial elements are septa sub-compact, free, straight or slightly curved. Septal apparatus organised in three size orders hierarchized in length and thickness. S3 septa are very short and are not always visible (Fig. 12A). Septa pennular. Septa of all size orders show numerous trabecular detachments near the inner edge. Elongated fossa inducing a bilateral symmetry. Endotheca made of dissepiments. Peripheral wall.

Dimensions. Calicular great diameter 4.8 to 8.2 mm — Calicular small diameter 4.2 to 6.1 mm — Septal density 4 to 6 septa per 2 mm.

Similarities and differences. See *T. termierorum* (Beauvais, 1986) below.

Stratigraphic and geographic distribution. Upper Sinemurian – Toarcian from Morocco (Middle and High Atlas Mountains), Pliensbachian from Afghanistan, Domerian from Slovenia.

Thecactinastraea termierorum (Beauvais, 1986)
Figures 13 and 14

* 1986 *Phacelophyllia termieri* sp. nov. — Beauvais, p. 39, Pl. 7 fig. 2, text-fig. 27.

2003 *Phacelophyllia termieri* Beauvais — Turnšek *et al.*, p. 297, Pl. 9 figs. 1–3.

2018 *Phacelophyllia termieri* Beauvais — Vasseur, p. 284-285, fig. 3.73.

v. 2019 *Phacelophyllia termieri* Beauvais — Boivin, p. 244, figs. 10.26–10.27.

Type designation. Holotype by original designation, MNHN.F.R11621.

Type locality and horizon. Lower Jurassic from Morocco (precise location unknown).

Originally included material. Only the holotype.

Etymology. Dedicated to Geneviève and Henri Termier. That is the reason why we emend the species name into a genitive plural (according to Articles 31.1.2 and 32.5 of the ICZN).

Material examined. 4 colonies: SB–55/3, SB–62, SB–200 and SB–379.

Ages and localities of material. Upper Sinemurian from Serdrar reef, Amellagou Region, High Atlas Mountains, Morocco.

Description. Colonies phaceloid with subparallel branches. Transverse section of corallites sub-circular or deformed by the intracalicular budding. Radial elements are septa sub-compact, joined, straight or curved. Septal apparatus organised in two or three size orders hierarchized in length but not in thickness. S1 septa are generally joined at their inner margins and reached the axial region. S2 septa are limited in length by the junction of the two neighbouring S1 septa. S3 septa are very short and are not always visible. Septa pennular. Few septa show trabecular detachments projecting into the axial region. Columella papillose. Epitheca made of dissepiments that can sometimes correspond on both side of a septum.

Dimensions. Calicular great diameter 5.9 to 7.7 mm — Calicular small diameter 4.5 to 7 mm — Septal density 5 to 8 septa per 2 mm. — Number of septa: 42 to 64 septa.

Similarities and differences. This species differs from *Thecactinastraea fasciculata* (Beauvais, 1986) that shows free septa and more trabecular detachments at inner margins of septa. *P. termierorum* differs from *P. bacari* (Turnšek, 2003) by the lower number of its septa and the higher size of its corallites.

Stratigraphic and geographic distribution. Lower Jurassic from Morocco, Upper Sinemurian from Morocco (High Atlas Mountains), Domerian from Slovenia, Toarcian from Morocco (High Atlas Mountains).

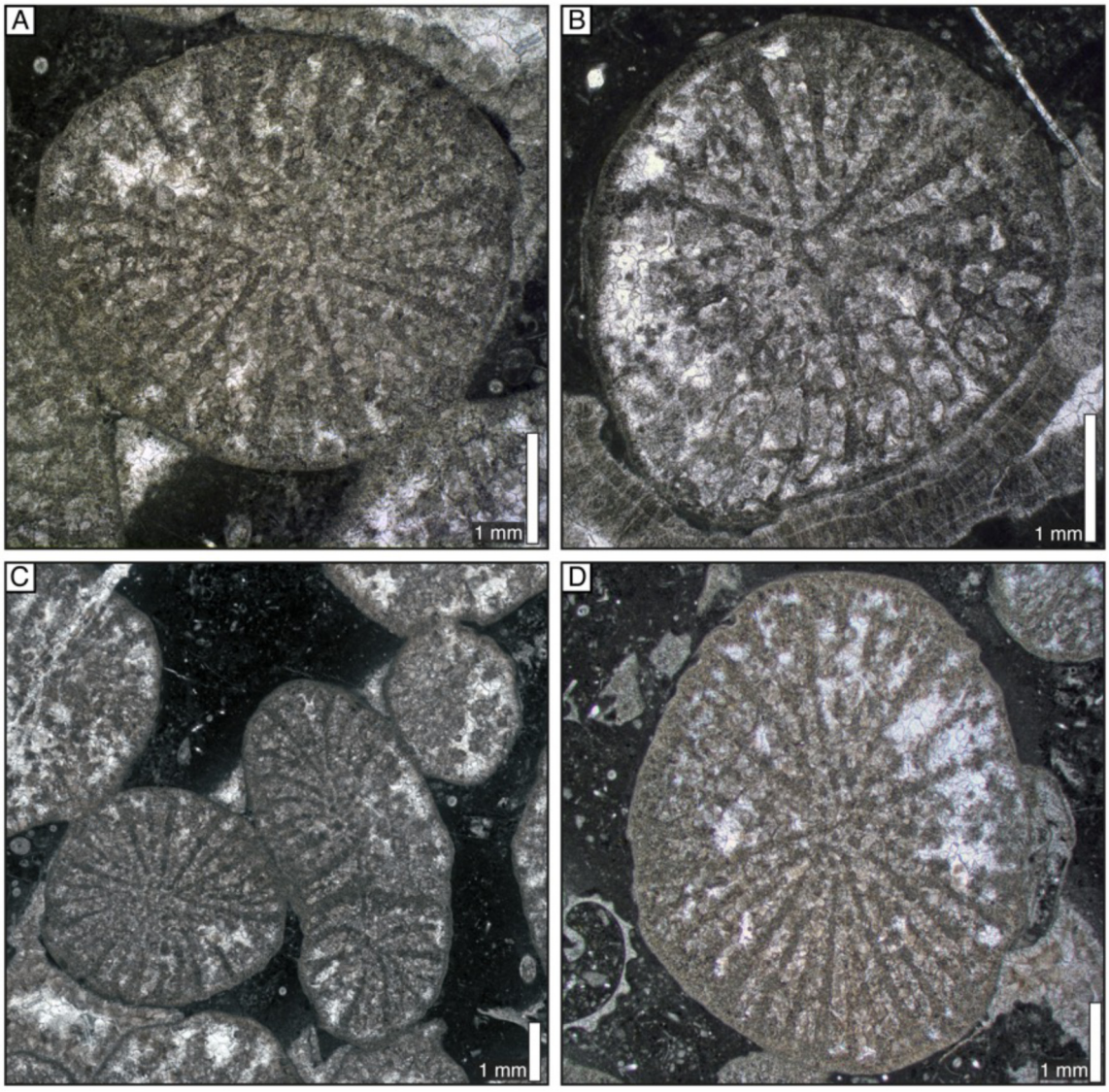

Fig. 14. *Thecactinastraea termierorum* (Beauvais, 1986). A–D Transverse thin sections of branches of the specimen SB–62.

Family **Cuifiidae** (Melnikova, 1975b) (= Coryphyllidae Beauvais, 1981)

Remark on the family name. Melnikova (1975b) created the family Cuifiidae with *Cuifia* as a type genus and *Cuifia gigantella* as the type species of the type genus. Cuif (1975a) created the genus *Coryphyllia*, which he subsequently placed within his new family Distichophyllidae in Cuif (1977). Beauvais (1981) created a new family Coryphyllidae with *Coryphyllia* as a type genus. Roniewicz (1989) used the latter family erected by Beauvais but as a subfamily (Coryphyllinae) including it within Reimaniphyllidae (Melnikova 1975) (senior synonym of Distichophyllidae). However, Roniewicz and Stanley (2009) redrew the boundaries of the Coryphylliidae to include both *Cuifia* and *Coryphyllia*. This nomenclatural act that contradicts the principle of priority was subsequently followed by various authors (Roniewicz 2010c, Bo *et al.*, 2017, Mannani 2020, Vasseur *et al.*, 2021, Vasseur and Lathuilière 2021). Then we re-establish here the priority of Cuifiidae over Coryphylliidae.

Genus ***Coryphyllia*** (Cuif, 1975a)

Type species. *Coryphyllia regularis* (Cuif, 1975b) by original designation.

Originally included species. Only the type species.

Similarities and differences. *Coryphyllia* differs from:

- *Cuifia* (Melnikova, 1975b) by the structure of wall, epithecal in *Coryphyllia* whereas *Cuifia* shows a peculiar segmented structure of wall. In absence of microstructure preserved, these two genera are distinguished here by the differences of size orders (6 in *Cuifia*) and the number of septa (between 120–160 septa and septal density of 3–5 septa per 1 mm in *Cuifia*).

- *Distichophyllia* (Cuif, 1975c) that is characterised by a mid-septal line in zigzag, which is expressed in the morphology of thin septa. Moreover, *Distichophyllia* shows a septal apparatus hierarchized in thick S1 and S2 septa whereas following size orders septa are thin.

- *Stylophyllopsis* (Frech, 1890) that is characterised by septal spines joined by stereome, often producing detachments

at the inner edge and a festooned transverse section in more outer position. The mid-septal line is very rare in *Stylophyllopsis*. The elongation of the fossa is also a good character for *Coryphyllia*.

Etymology. From *coryphe*: crest and *phyllia*: leaf both in ancient Greek.

Status. Available and valid.

Coryphyllia capillaria (Vasseur and Lathuilière, 2021)
Figure 15

v. 2018 *Coryphyllia* sp. 1 — Vasseur, p. 152-153, fig. 3.19.

v. 2019 *Coryphyllia capillaria* Vasseur & Lathuilière — Boivin, p. 192, fig. 10.4.

*v. 2021 *Coryphyllia capillaria* sp. nov. — Vasseur & Lathuilière, p. 1211, fig. 15.

Type designation. Holotype by original designation, CPUN PFPyr 7-2 *in* (Vasseur and Lathuilière 2021), the name was not available in Boivin (2019) ICZN art. 8.3.

Type locality and horizon. Pliensbachian from Estivère Pass, French Pyrenees.

Originally included material. Eight paratypes: CPUN 2303A1-2, CPUN 2303A8-1, CPUN AM16183-4, CPUN CDAm7, CPUN MA0504E7-13, CPUN MA0504E7-17, CPUN MA0704E3-10, CPUN MA0704E3-12.

Etymology. From *capillus*: hair in Latin referring to the very thin and long septa of high orders.

Material examined. 6 specimens: SB–230/1, SB–223, SB–244, SB–249, SB–341 and SB–346/1, and 1 uncertain silicified specimen: SB–68.

Ages and localities of material. Upper Sinemurian from Serdrar reef and lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Solitary coral, conical, transverse section of corallite subcircular to slightly elliptical. Costosepta organised in a regular septal apparatus of three or four size orders difficult to distinguish. Septa are mostly straight or curved according to the bilateral symmetry, compact, free, slightly attenuated at inner margin. Lateral faces are weakly granulated. Endotheca made of abundant vesicular dissepiments regularly distributed in the interseptal space. Elongated fossa.

Dimensions. Calicular diameter 25 to 33 mm — Septal density 4 to 12 septa per 5 mm.

Similarities and differences. See *C. regularis* below.

Stratigraphic and geographic distribution. Sinemurian — Pliensbachian from Morocco (Middle and High Atlas Mountains), Pliensbachian from France (Pyrenees).

Coryphyllia regularis (Cuif, 1975a)
Figure 16

* 1975a *Coryphyllia regularis* sp. nov. — Cuif, p. 380, fig 37 a–c, fig. 38.

1984 *Coryphyllia regularis* Cuif — Ramovš & Turnšek, p. 175, Pl. 4 fig. 1.

1989 *Coryphyllia regularis* Cuif — Turnšek & Buser, p. 84, Pl. 3.

1994 *Coryphyllia regularis* Cuif — Turnšek & Senowbari-Daryan, p. 481, Pl. 3 fig. 5.

2013 *Coryphyllia regularis* Cuif — Liao & Deng p. 54, Pl. 20 fig. 4. v. 2018 *Coryphyllia regularis* Cuif — Vasseur, p. 194-195, fig. 10.5.

v. 2019 *Coryphyllia regularis* Cuif — Boivin, p. 194–195, figs. 10.5.

v. 2021 *Coryphyllia regularis* Cuif — Vasseur & Lathuilière, p. 1214, fig. 16.

Type designation. Holotype by original designation. MNHN.F.A31946; (Cuif, 1975a): p. 379, fig. 37 a, b? and c?

Type locality and horizon. Lower Norian from Valley Alakir Cay, Taurus Mountains, Turkey.

Originally included material. Cuif (1975a) specified that several specimens are included in the species but no further detail is given.

Etymology. From *regularis* in Latin referring to the regularity of the septal apparatus.

Material examined. 5 specimens: SB–69, SB–140, SB–146/1, SB–242/1 and SB–316/1 and 3 uncertain specimens: SB–145/1, SB–248 and SB–251.

Ages and localities of material. Upper Sinemurian from Serdrar reef, upper Sinemurian or lowermost Pliensbachian from Castle olistolith and lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Solitary coral, transverse section of corallite circular to elliptical. Radial elements are septa (costae not visible) organised in a regular septal apparatus of three size orders. Septa are straight or curved, compact, free, sometimes contratingent, attenuated at inner margin, often rhopaloid. Lateral faces are ornamented with granules of low relief. Inner margin of septa is smooth. Vestiges of a wavy mid-septal line often visible. Columella absent, the fossa is tight and elongated (notably in elliptical corallite), defining the apparent bilateral symmetry of the corallite. Endotheca typical for this species, made of abundant vesicular dissepiments regularly distributed in the interseptal space.

Dimensions. Calicular great diameter 14.5 to 40 mm — Calicular small diameter 12.75 to 38 mm — Septal density 3 to 8 septa per 5 mm.

Similarities and differences. *Coryphyllia regularis* differs from:

- *Coryphyllia capillaria* (Vasseur and Lathuilière, 2021) by its lower number of septa, its lower septal density, and the size orders of its septal apparatus better hierarchized.

- *Coryphyllia subregularis* (Beauvais, 1986) that shows equivalent dimensions, differs by a less regular septal apparatus and larger dissepiments, and possibly a lacking epitheca.

- *Coryphyllia bicuneiformis* (Melnikova 1975 Vasseur and Lathuilière, 2021 Vasseur and Lathuilière, 2021) has a smaller diameter, more bicuneiform septa and a more elongated calice.

Stratigraphic and geographic distribution. Upper Triassic from China, Greece, Turkey and Slovenia, Sinemurian and Pliensbachian from Morocco (Middle and High Atlas Mountains).

Coryphyllia subregularis ? (Beauvais, 1986)
Figure 17

?p *Stylophyllopsis mojsvari* sp. nov. — (Frech, 1890), p. 52, Pl. 10 figs. 7—8, non figs. 9—14.

* 1986 *Coryphyllia subregularis* sp. nov. — Beauvais, p. 23, Pl. 4 fig. 3. v. 2018 *Coryphyllia subregularis* Beauvais — Vasseur, p. 156–157, fig. 3.21.

v. 2019 *Coryphyllia subregularis* Beauvais — Boivin, p. 196, figs. 10.6.

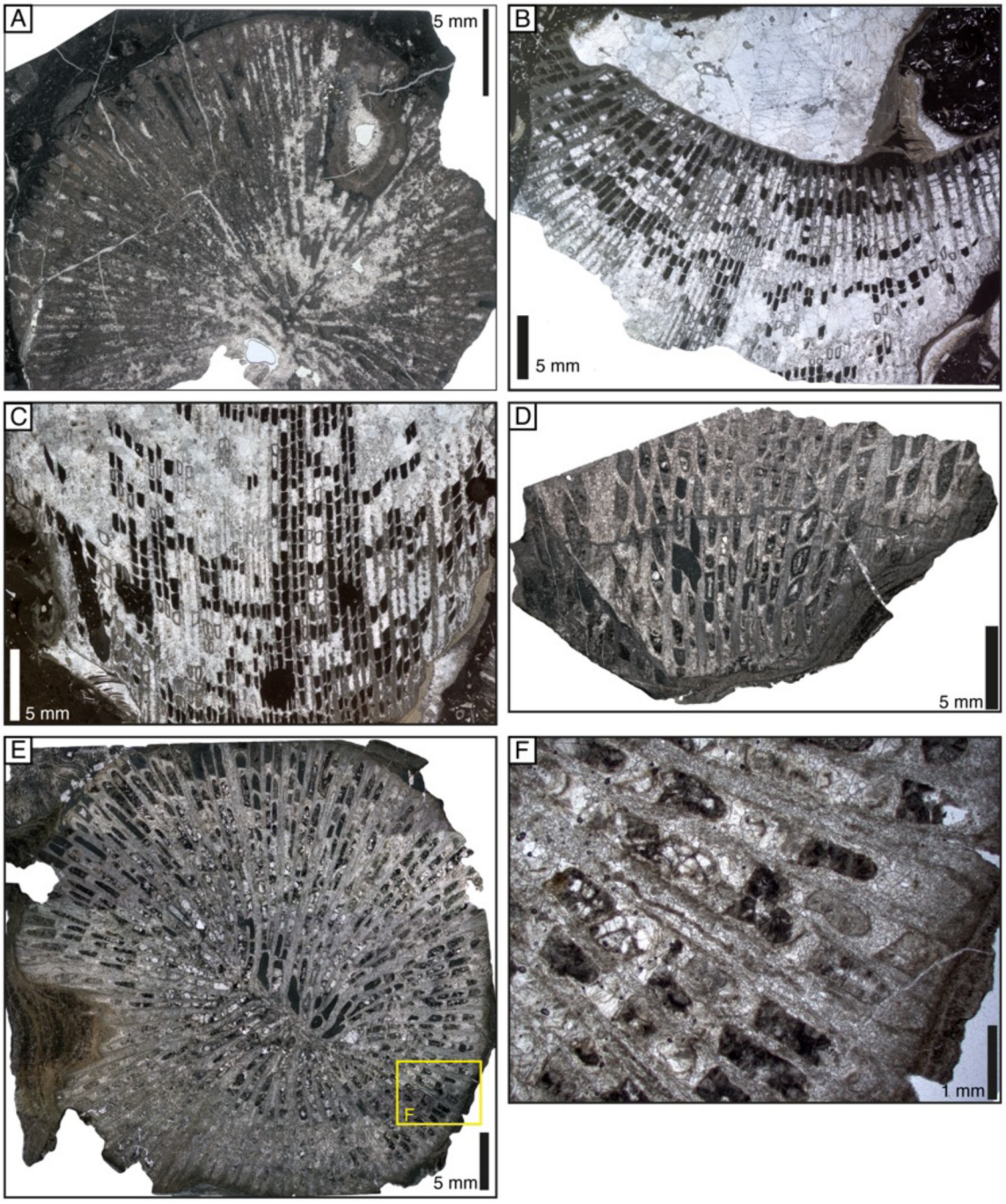

Fig. 15. *Coryphyllia capillaria* (Vasseur and Lathuilière, 2021). A Transverse thin section of the specimen SB–244. B–C Longitudinal thin section of the specimen SB–230/1, section B distal and section C proximal. D Longitudinal thin section of the specimen SB–214. E Transverse thin section of the specimen SB–214. F Enlargement of E. Note the mid-septal line.

2021 *Coryphyllia subregularis* Beauvais — Vasseur & Lathuilière, p. 1214, fig. 17.

Type designation. Holotype by original designation MNHN.F.R11609; Beauvais, p. 23, Pl. 4, fig. 3.

Type locality and horizon. Domerian, *Fuciniceras cornacaldense* horizon, from Jebel el Kounif (Bou-Arfa Range), Morocco.

Originally included material. No mentioned material other than the holotype.

Etymology. From *sub*: close to in Latin referring to the proximity with the species *C. regularis.*

Material examined. 1 uncertain specimen: SB–169/2.

Ages and localities of material. Upper Sinemurian or lowermost Pliensbachian from Castle olistolith, High Atlas Mountains, Morocco.

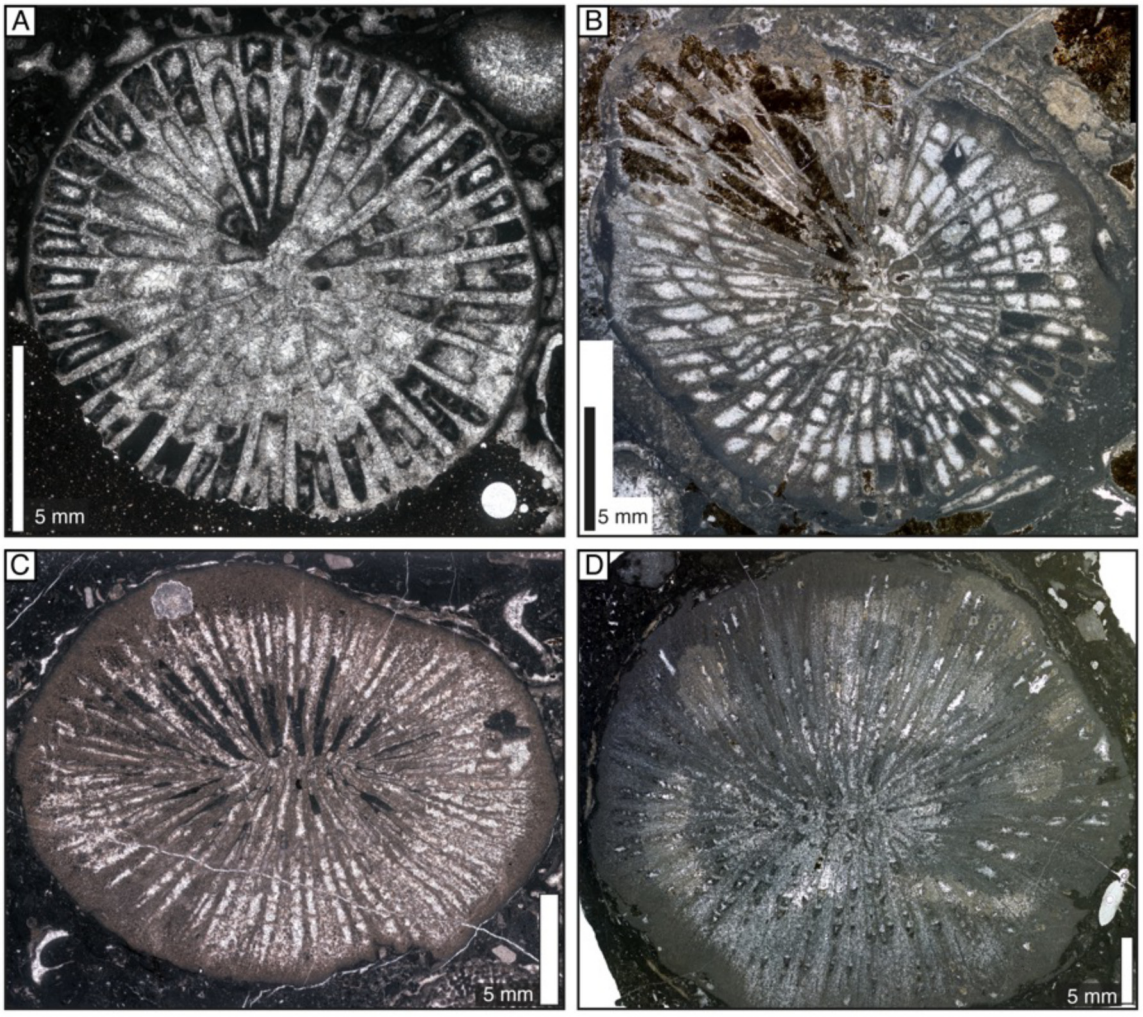

Fig. 16. *Coryphyllia regularis* (Cuif, 1975a). A Transverse thin section of the specimen SB–69. B Transverse thin section of the specimen SB–146/1. C Transverse thin section of the specimen SB–316/1. D Transverse thin section of the specimen SB–242/1.

Description. Solitary coral. Septal apparatus regular. Septa are straight or curved, compact, sometimes contratingent, often rhopaloid. Endotheca made of large vesicular dissepiments regularly distributed in the interseptal space.

Dimensions. Septal density 4-5 septa per 5 mm.

Similarities and differences. This species is close to *Coryphyllia regularis* (Cuif, 1975a) and shows equivalent dimensions, but differs by a less regular septal apparatus and larger dissepiments. For comparison with other species, see *C. regularis*.

Stratigraphic and geographic distribution. Rhaetian from Austria? Upper Sinemurian – Pliensbachian from Morocco Middle and High Atlas Mountains.

Genus ***Paracuifia*** (Melnikova, 2001)

Type species. *Protoheterastraea magnifica* (Melnikova, 1984) by original designation, p. 44.

Originally included species. *Paracuifia magnifica* (Melnikova, 1984) and *Paracuifia tortuosa* (Melnikova, 2001).

Similarities and differences. *Paracuifia* is the single genus of Cuifiidae that shows phaceloid colonies. For comparisons with similar genera, see genus *Thecactinastraea*.

Etymology. From *para*: nearly in ancient Greek and *cuifia* referring to the genus *Cuifia*.

Status. Available and valid.

Paracuifia castellum sp. nov.

Figure 18

Type designation. Holotype designated herein: SB–78/1 (20 thin sections: SB–78A to SB-78F, SB–78H to SB-78U).

Type locality and horizon. Upper Sinemurian or lowermost Pliensbachian from Castle olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Originally included material. Only the holotype.

Etymology. From *castellum*: castle in Latin referring to the Castle olistolith named after the Berber ruins located just above the reef.

Diagnosis. *Paracuifia* with circular or slightly subcircular corallite about one centimetre in diameter, and around thirty septa.

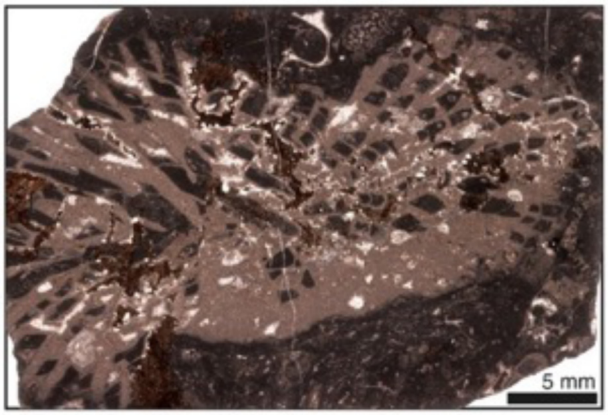

Fig. 17. *Coryphyllia subregularis* ? (Beauvais, 1986). Oblique thin section of the specimen SB–169/2.

Description. Colony phaceloid. Corallite circular or slightly subcircular. Septa thick, compact along the entire length, free or joined, straight or slightly undulated. Septal apparatus ordered in two size orders. Lateral margin of septa without ornamentation. Ghost of microstructure characterised by an aligned set of brown dots in the mid septal plan (Fig. 18F). Mid-septal line straight to slightly wavy (Fig. 18E). Endotheca made of large dissepiments regularly distributed in the interseptal space. These dissepiments show the same microstructure as septa (Fig. 18B), which indicated that the septa would be mostly made of thickening deposits. Columella absent. Costae absent. Probably trabeculothecal wall (Fig. 18E).

Dimensions. Calicular diameter 9.2 to 11.5 mm — Number of septa 30 septa — Septal density 2 to 3 septa per 3 mm.

Similarities and differences. *Paracuifia castellum* sp. nov. differs from:

— *Paracuifia magnifica* (Melnikova, 1984) that has an elliptic shape of corallites, a diameter from 6 mm in juvenile stage to 40 mm, and a number of septa around 200 in 5 size orders in adult stage.

— *Paracuifia tortuosa* (Melnikova, 2001) that has an elliptic shape of corallites, a diameter from 8 to 40 mm, and 130 to 150 septa in four size orders.

— *Paracuifia smithi* (Caruthers and Stanley, 2008) that has a very large and irregular corallite, a diameter from 10 to 23 mm, a tendency to be pseudo-meandroid, and poorly developed S2 septa.

— *Paracuifia jennieae* (Caruthers and Stanley, 2008) that has a pseudo-meandroid arrangement and a septal apparatus organised in four size orders.

— *Paracuifia anomala* (Caruthers and Stanley, 2008) that shows a cerioid arrangement of corallites.

Stratigraphic and geographic distribution. Upper Sinemurian or lowermost Pliensbachian from Morocco (High Atlas Mountains).

Family **Dermosmiliidae** (Koby, 1889)

Genus ***Proleptophyllia*** (Alloiteau, 1952)

Type species. *Montlivaultia granulum* (Fromentel and Ferry, 1866) by monotypy.

Similarities and differences. The genus *Proleptophyllia* differs from other Moroccan Lower Jurassic solitary genera by the moniliform character of the distal edge of septa.

Remarks. Following Vasseur and Lathuilière (2021), we have assumed the synonymy between *Proleptophyllia* and *Epiphyllum* (Alloiteau, 1957), and we have also included *Cyclophyllopsis cornutiformis* (Beauvais, 1986) in the synonymy of the species.

Etymology. From *pro*: before in ancient Greek and *leptophyllia* referring to the genus *Leptophyllia* (Reuss, 1854).

Status. Available and valid.

Proleptophyllia granulum (Fromentel and Ferry, 1866) Figure 19

*v. 1866 *Montlivaultia granulum* sp. nov. — Fromentel & Ferry, p. 136, pl. 24 fig. 2.

1866 *Montlivaultia arenula* sp. nov. — Fromentel & Ferry, p. 134-135, pl. 23 fig. 4.

1952 *Proleptophyllia granulum* (Fromentel & Ferry) — Alloiteau, p. 666.

1956 *Proleptophyllia granulum* (Fromentel & Ferry) — Alloiteau, Pal. univers. n○ 121.

1957 *Epiphyllum arenula* (Fromentel & Ferry) — Alloiteau, p. 107, pl. 5 fig. 13.

1957 *Proleptophyllia granulum* (Fromentel & Ferry) — Alloiteau, p. 113, pl. 8 fig. 10, and fig. 73.

1986 *Cyclophyllopsis cornutiformis* nov. sp. — Beauvais, p. 34, pl. 7 fig. 1, pl. 8 fig. 1, text-fig. 23.

2011 *Proleptophyllia cf. granulum* (Fromentel & Ferry) — Lathuilière, p. 542, pl. 3 fig. 11–12.

.2018 *Proleptophyllia granulum* (Fromentel & Ferry) — Vasseur, p. 297–298, fig. 3.78.

v. 2019 *Proleptophyllia granulum* (Fromentel & Ferry) — Boivin, p. 254–255, figs. 10.31.

2021 *Proleptophyllia granulum* (Fromentel & Ferry) — Vasseur & Lathuilière, p. 1222, fig. 23.

Type designation. Lectotype MNHN.F.M03533, by inference from a holotype by Alloiteau (1956) (ICZN art 74.6).

Type locality and horizon. Pliensbachian from May-sur-Orne, Normandy, France.

Originally included material. Unspecified.

Etymology. From *granulum*: small grain in Latin referring to the shape of distal edge of septa.

Material examined. 2 specimens: SB–167/1 and SB–342 and 1 uncertain specimen: SB–326/1.

Ages and localities of material. Upper Sinemurian or lowermost Pliensbachian from Castle olistolith and lower Pliensbachian from Owl olistolith (and possibly upper Sinemurian from Serdrar reef), Amellagou Region, High Atlas Mountains, Morocco.

Description. Solitary coral. Transverse section of corallite sub-circular to slightly elliptical. Septa sub-compact with pennular structure, straight or slightly wavy, joined or contratingent. Hexameral symmetry. Septal apparatus organised in four size orders. Pennulae-like granules are not arranged in menianae and do not alternate between neighbouring septa. Trabecular axes are more and more detached toward the centre of corallite producing a parietal papillose columella.

Dimensions. Calicular diameter 18.7 to 19.7 mm — Number of septa 120 septa — Septal density 10 to 12 septa per 5 mm.

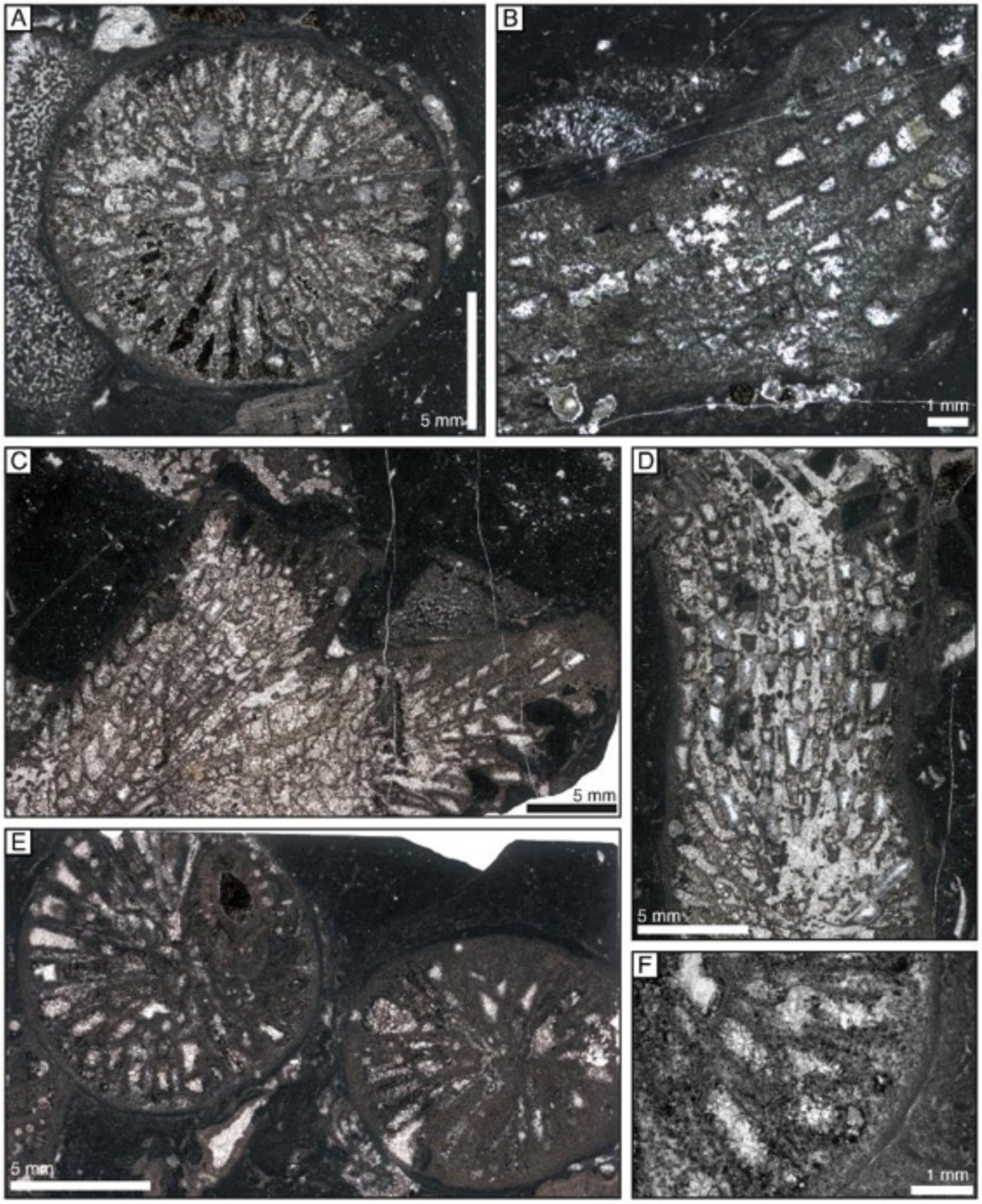

Fig. 18. *Paracuifia castellum* sp. nov. A & E transverse section of branches of the holotype SB–78/1. B–D longitudinal section of branches of the holotype SB–78/1. F Enlargement of E.

Stratigraphic and geographic distribution. Upper Sinemurian — lower Pliensbachian from Morocco, Pliensbachian from France, Domerian from Morocco, Toarcian from Morocco.

Family **Latomeandridae** (Alloiteau, 1952)
Genus ***Periseris*** (Ferry, 1870)

Type species. *Agaricia elegantula* (Orbigny, 1850) by monotypy.

Similarities and differences. This genus differs from *Thamnasteria* (Le Sauvage, 1823) by the septal structure, typically alternating pennular in *Periseris* with pennular rims turned upward. A complete comparison is available in Lathuilière (1990, p. 36). The differences with *Thamnaster-*

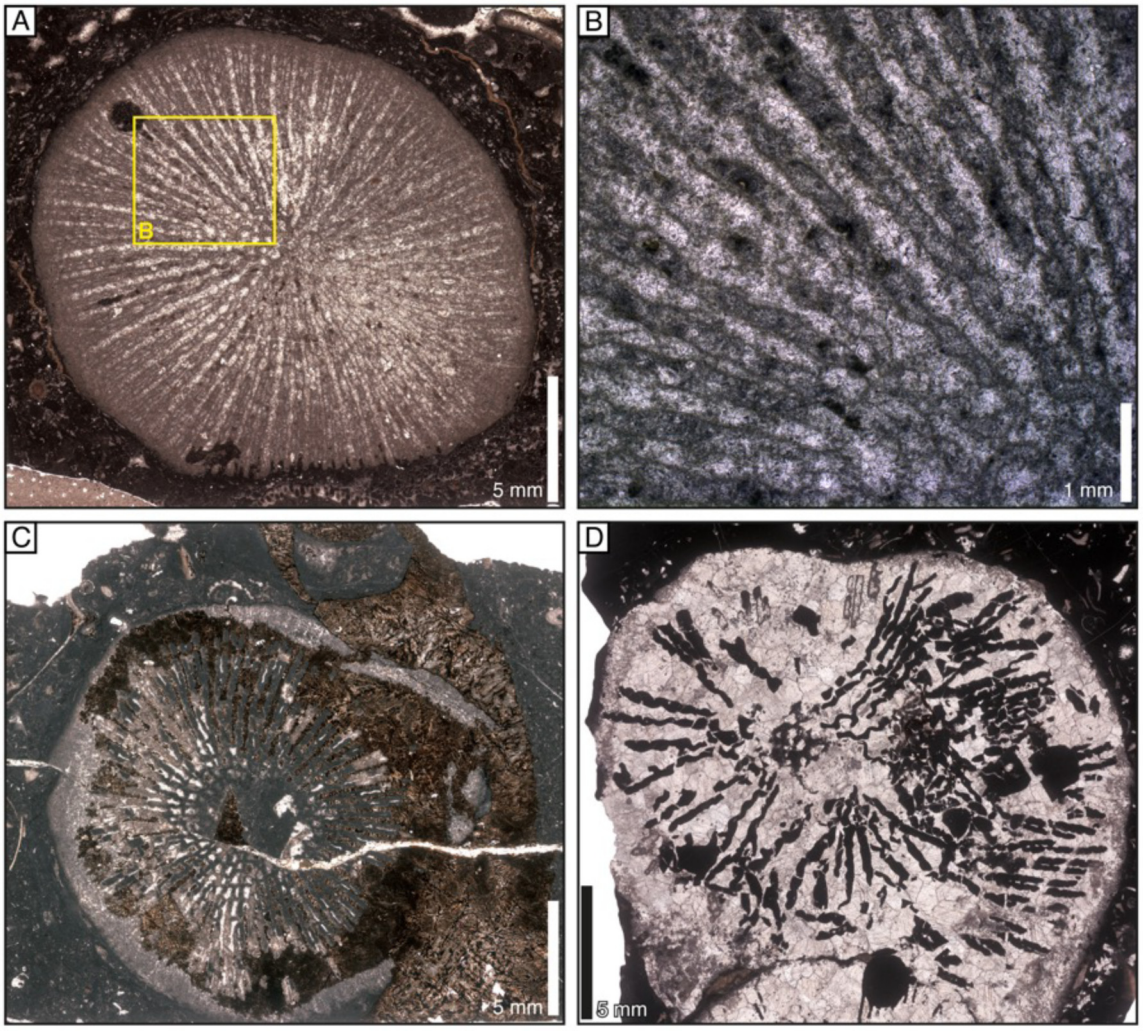

Fig. 19. *Proleptophyllia granulum* (Fromentel and Ferry, 1866). A Transverse thin section of the specimen SB–342. B Enlargement of A showing the septal ornamentation. C Distal transverse section of the specimen SB–167/1. *Proleptophyllia granulum*? (Fromentel and Ferry, 1866).
D Transverse section of the badly preserved specimen SB–326/1.

iamorpha (Melnikova, 1971), a Triassic genus, is still a matter of discussion (Lathuilière, 1990).

Etymology. From *peri*: around in ancient Greek and *series*: row in Latin probably referring to the meandroid tendency of the genus with concentric valleys.

Status. Available and valid.

Periseris elegantula (Orbigny, 1850)
Figure 20

* 1850 *Agaricia elegantula* sp. nov. — Orbigny, p. 293.
1990 *Periseris elegantula* (Orbigny) — Lathuilière, p. 38 Pl. 1–5, with synonymy (50 references).
1993 *Periseris elegantula* (Orbigny) — Pandey & Fürsich, p. 37, Pl. 11 fig. 2, text-fig 22.
2000 *Periseris elegantula* (Orbigny) — Lathuilière, p. 157–159, fig. 13.1–2.
2003 *Periseris elegantula* (Orbigny) — Pandey & Fürsich, p. 94, Pl. 26 fig. 1–6.
2005 *Periseris elegantula* (Orbigny) — Morycowa & Misik, p. 430, fig. 8.1–4.
? 2006 *Periseris elegantula* (Orbigny) — Pandey & Fürsich, p. 65, Pl. 5 fig. 4–7.
? 2011 *Periseris* sp. — Lathuilière, p. 540, Pl. II, figs. 5–9.
2018 *Periseris elegantula* — Vasseur, p. 277–278, fig. 3.70.
2019 *Periseris* sp. — Brame *et al.*, fig. 7.F–G.
v. 2019 *Periseris elegantula* (Orbigny) — Boivin, p. 236-237, figs. 10.24.
v. 2023 *Periseris elegantula* (Orbigny) — Lathuilière *et al.*, p. 30, fig. 9.C–D.

Type designation. Lectotype, by inference of a holotype by (Alloiteau, 1957) (ICZN art 74.6), MNHN.F.A26574.

Type locality and horizon. Bajocian from Langres, Haute-Marne, France.

Originally included material. Unspecified.

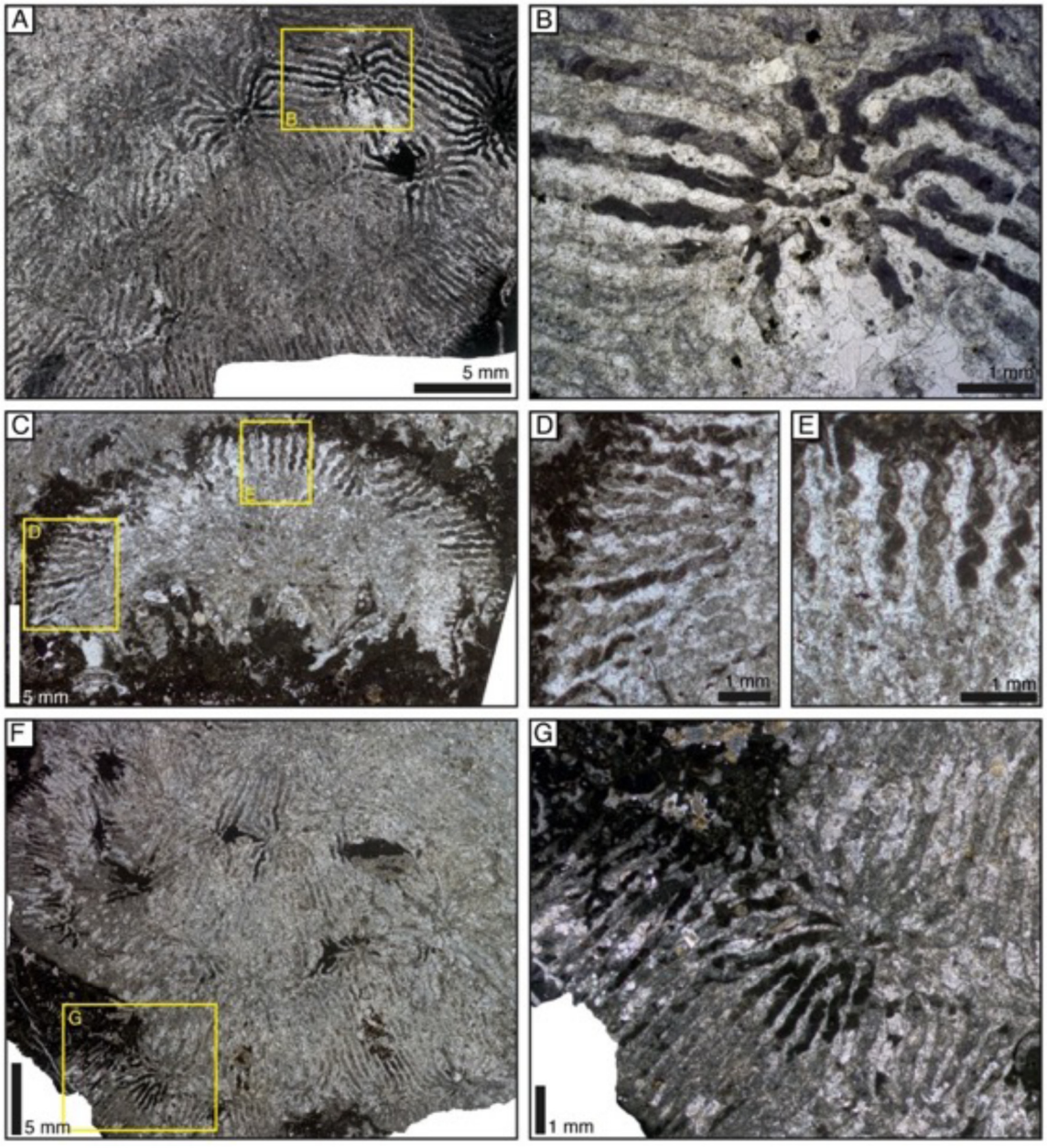

Fig. 20. *Periseris elegantula* (Orbigny, 1850). A Transverse thin section of the specimen SB–345. B Enlargement of A. C Longitudinal thin section of the specimen SB–345. D–E Enlargements of C. F Transverse thin section of the specimen SB–237. G Enlargement of F.

Etymology. From *elegans*: elegant and *ula:* a diminutive suffix in Latin.

Material examined. 2 colonies: SB–237 and SB–345.

Ages and localities of material. Lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Flat or flattened hemispheric thamnasterioid colonies. Radial elements are biseptal sheets, thick, exactly confluent, subcompact, straight or sinuous, free or joined, sometimes contratingent. Pennular structure of radial elements, sub-continuous meniana with pennular rims turned upward (Fig. 20E,F). Pennulae of one septum alternate with those of the neighbouring septa. On both sides on a same septum, pennulae are not always aligned. Biseptal sheets show a sub-parallel preferential orientation between corallites (Fig. 20A). No hexameral symmetry visible. Endotheca badly preserved, perhaps made of vesicular dissepiments. Columella styliform. No wall. Remains of a holotheca are locally preserved (Fig. 20F).

Dimensions. Distance from corallite to corallite 3.6 to 7.8 mm — Septal density 4 to 6 septa per 2 mm.

Similarities and differences. *Periseris elegantula* is the only nominal species of the genus known for the Liassic. However, a *Periseris* sp. was described in Toarcian from Morocco (Lathuilière, 2011). It was kept in open nomenclature for its absence of holotheca.

Stratigraphic and geographic distribution. Pliensbachian and Toarcian from Morocco (High Atlas Mountains), Bajocian of France, Belgium, Luxembourg, Germany, Switzerland, Slovakia, Bathonian of India, Dogger from Iran.

The new discovery of such an ancient occurrence fills the gap between the genus *Periseris* and the closely related Triassic genus *Thamnasteriamorpha* (Melnikova, 1971) (=*Thamnotropis* Cuif, 1975b).

Family **Protoheterastraeidae** (Cuif, 1977)

Genus ***Paravolzeia*** (Roniewicz *et al.*, 2005)

Type species. *Paravolzeia alpina* (Roniewicz *et al.*, 2005) nomen novum pro *Volzeia* (*Hexastraea*) *fritschi* (Volz, 1896) in (Cuif, 1975a), non *Hexastraea fritschi* (Volz, 1896), by original designation.

Originally included species. *Paravolzeia alpina* (Roniewicz *et al.*, 2005) and *Paravolzeia timorica* (Roniewicz *et al.*, 2005).

Similarities and differences. This genus differs from the phaceloid genera:

- *Paracuifia* (Melnikova, 2001) that has a vesicular endotheca, and poorly hierarchised septa.
- *Thecactinastraea* (Beauvais, 1986) that has septa much more ornamented.
- *Phacelostylophyllum* (Melnikova, 1972) that is stylophyllid in septal structure.
- *Retiophyllia* (Cuif, 1966) that is a distichophylliid in structure and shows a typical epitheca.

Etymology. From *para*: near in ancient Greek, and *volzeia* referring to the similarity with the genus *Volzeia* (Cuif, 1966).

Status. Available and valid.

***Paravolzeia? alpina*?** (Roniewicz *et al.*, 2005)

Figure 21

1975a *Volzeia* (*Hexastraea*) *fritschi* sp. nov. — Cuif, p. 352, figs. 25-26 (non *Hexastraea fritschi* (Volz, 1896), p. 91, Pl. 11 figs. 14–20).

* 2005 *Paravolzeia alpina* sp. nov. — Roniewicz *et al.*, p. 293. fig. 4–D, G.

2015 *Paravolzeia alpina* Roniewicz *et al.* — Stanley & Onoue, p. 21, fig. 15–a,b.

v. 2019 *Paravolzeia*? sp. — Boivin, p. 234, fig. 10.23.

Type designation. Roniewicz *et al.* (2005) strangely mentioned a lectotype for the creation of their own species. The "lectotype" would be housed in MNHN and implicitly referred to the material of Cuif (1975a). Unfortunately, in the Corallosphere website (Roniewicz, 2013), a holotype housed in Warsaw ZPAL HVIII/1 and figured in Roniewicz *et al.* (2005) fig. 4D, G is mentioned in contradiction with the previous designation.

Type locality and horizon. Carnian, Julian sub-stage, from Dolomites, northern Italy.

Originally included material. Only the type specimen?

Etymology. From *alpina* referring to the Alps.

Material examined. 1 sample: SB–219/2.

Ages and localities of material. Upper Sinemurian from Serdrar reef, Amellagou Region, High Atlas Mountains, Morocco.

Description. Fragment of colony, perhaps phaceloid. Septa thin, compact, free, sinuous. Septal apparatus organised in three size orders. S1 septa reach the centre of the corallite. Among them, some septa show a spoon-shaped inner margin, they could correspond to the six protosepta (?). S2 measure two thirds of the radius of the corallite in length. S3 are short and not always present. Lateral faces of septa lowly ornamented with possible granules. Fossa straight and narrow defining bilateral symmetry. Endotheca present made of few thin tabulae.

Dimensions. Calicular diameter circa 3 mm — Number of septa circa 30 septa extrapolated from the best-preserved sector — Septal density 3 septa per 1 mm.

Remarks. The only fragment found does not allow a firm identification.

Similarities and differences. *Paravolzeia alpina* (Roniewicz *et al.*, 2005) differs from *P. timorica* (Roniewicz *et al.*, 2005) that has a smaller calicular diameter (from 1.8 to 3 mm) and a poorly developped septal apparatus.

Stratigraphic and geographic distribution. Carnian from Dolomites (Italy), Norian from Japan, Sinemurian from Morocco?

Family **Reimaniphylliidae** (Melnikova, 1975b)

Genus ***Distichophyllia*** (Cuif, 1975a)

Type species. *Montlivaltia norica* (Frech, 1890): p. 39, pl. 3 fig. 8–9, pl. 10 fig. 1–5. pl. 18 fig. 7. by original designation.

Originally included species. Only the type species.

Similarities and differences. Differs from *Coryphyllia* by the microstructure of septa characterised by a mid-septal line in zigzag and fibrous, and laminar thickening deposits. In absence of preserved microstructure, the distinction remains difficult and we can suspect some inappropriate identifications (for instance in Deng and Zhang, 1984b). Moreover, *Distichophyllia* shows a septal apparatus hierarchized in thick S1 and S2 septa whereas following size orders septa are thin. Similar genera are compared in the paragraph similarities and differences of the genus *Coryphyllia.*

Etymology. From *distichos*: double row and *phyllia*: leaf both in ancient Greek, probably referring to usage in botany to designate a particular kind of phyllotaxy very similar to the structure of trabecular axes.

Status. Available and valid.

Distichophyllia norica (Frech, 1890)

Figure 22

1854 *Montlivaltia cupuliformis* n. sp. non Edwards & Haime — Reuss, p. 102, Pl. 6 figs. 16–17.

* 1890 *Montlivaltia norica* nomen novum — Frech, p. 39-40, Pl. 3 fig. 9, Pl. 10 figs. 1–5, Pl. 13 figs. 1–7, Pl. 18 fig. 17.

1890 *Montlivaltia gosaviensis* n. sp. — Frech, p. 41, Pl. 11 fig. 7.

1903 Montlivaltia aff. *norica* Frech — Kittl, p. 727 and 731.

? 1911 *Montlivaltia norica* Frech — Vinassa de Regny p. 99, Taf. 71, Fig. 15–17.

non 1911 *Montlivaltia gigas* sp. nov. (non Fromentel 1861) — Vinassa de Regny, p. 98, Pl. 70 figs. 12–13.

1927 *Montlivaultia norica* Frech — Smith, p. 126, Pl. 111 fig. 6.

1929 *Montlivaltia norica* Frech— Douglas, p. 645, PI. 46, figs. 1a, 1b, & 2.

1956 *Montlivaltia norica* Frech — Squires, p. 21, figs. 32–47.

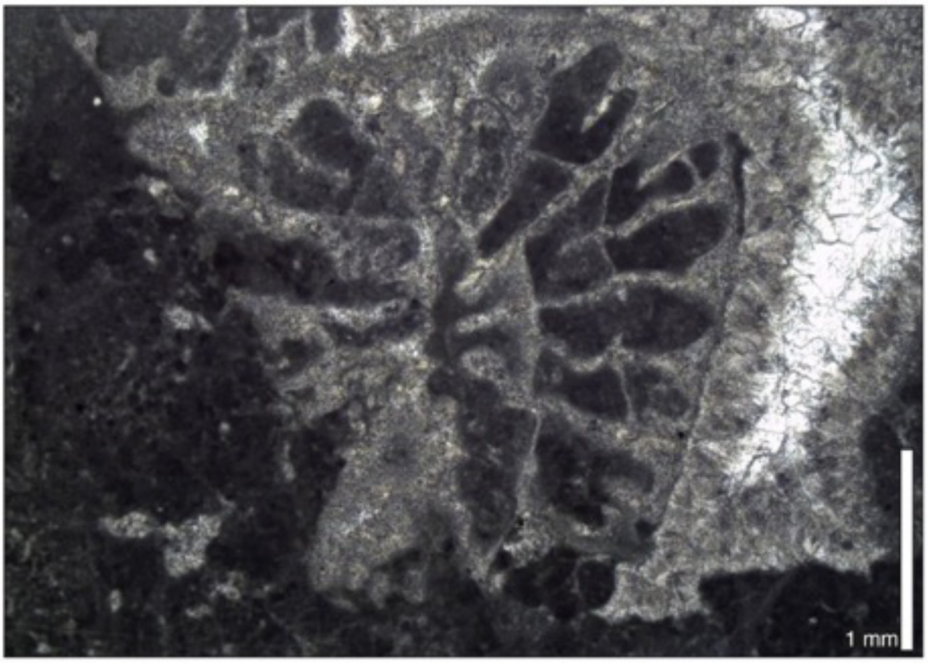

Fig. 21. *Paravolzeia*? *alpina*? (Roniewicz *et al.*, 2005). Transverse thin section of the specimen SB–219/2.

? 1964 *Montlivaltia* sp. *cf. M. norica* Frech — Kanmera & Furukawa, p. 120, Pl. 12 figs. 6–10.

1966a Montlivaltia norica Frech — Kolosváry, p. 182.

1966b Monilivaltia norica Frech — Kolosváry, p. 127.

1975a *Distichophyllia norica* (Frech) — Cuif, p. 304-318, 398, figs. 2–6.

1975 *Reimaniphyllia gosaviensis* (Frech) — Melnikova, p. 87–89, Pl. 15 figs. 1 and ? 2.

? 1975 *Montlivaltia norica* Frech — Wu, p. 106, Pl. 4 figs. 6–7.

1977 *Distichophyllia norica* (Frech) — Cuif, p. 19, 39, fig. 4, Pl. 3 figs. 4–8, Pl. 4 figs. 5–7, Pl. 5 fig. 3.

p 1979 *Montlivaltia norica* Frech — Schäfer, p. 44, Pl. 10 fig. 1 ?, Pl. 11 fig. 2.

1979 "*Montlivaltia*" *norica* Frech — Stanley, p. 12, 24, 28, 32, 38.

? 1979 *Disticophyllia cf. norica* (Frech) — Montanaro Gallitelli, Russo, & Ferrari, p. 149, pl. 4 fig. 9 a–b.

1979 *Montlivaltia norica* Frech— Liao & Li, p. 53, Pl. 24 figs. 7–11.

? 1980 *Montlivaltia norica* Frech — Senowbari-Daryan, p. 39, Pl. 4 fig. 1.

? 1980 *Montlivaltia norica* Frech — Kristan-Tollmann *et al.*, p. 173, Pl. 5 fig 6, Pl. 6 figs. 1, 3.

1980 *Distichophyllia norica* (Frech) — Cuif, p. 365, fig. 3.

1981 Montlivaltia norica Frech — Sadati, p. 199.

1982 Montlivaltia norica Frech — Berg & Cruz, p. 11.

? 1982 *Montlivaltia norica* Frech — Liao, p. 169, pl. 16 fig. 2a–c.

1982 Distichophyllia norica (Frech) — Buser *et al.*, p. 21.

p 1984a *Distichophyllia norica* — Deng & Zhang, p. 261, Pl. 5 fig. 3? non fig. 2.

1984a *Distichophyllia norica xizangensis* (subsp. nov.) — Deng & Zhang, p. 261, Pl. 5 figs. 6–9.

1984a *Montlivaltia tenuise* (sp. nov.) — Deng & Zhang, p. 246, Pl. 2 figs. 3–6.

? 1984b *Distichophyllia cf. norica* — Deng & Zhang, p. 293, Pl. 4 fig. 3.

1985 Distichophyllia norica (Frech) — Bychkov & Melnikova, p. 161.

? 1986 *Distichophyllia norica* (Frech) — Stanley & Senowbari-Daryan, p. 173, fig. 3.

p 1986 *Distichophyllia norica* (Frech) — Stanley, p. 29, Pl. 3.1 figs. 4 and 6 non 5.

? 1986 *Distichophyllia norica* Frech — Xia & Liao, p. 44, Pl. 3 figs. 5–12.

1986 *Distichophyllia cf. norica* (Frech) —Melnikova & Bychkov, p. 65, Pl. 6 fig. 2,.

1986 *Distichophyllia norica* Frech — Iljina & Melnikova, p. 46, Pl. 12 fig. 1–2.

non 1986 *Distichophyllia cf. norica* Frech — Iljina & Melnikova, Pl. 18 fig. 1.

1987 *Distichophyllia gosaviensis* (Frech) — Turnšek & Ramovš, p. 35, Pl. 4 figs. 5–6.

1989 *Distichophyllia norica* (Frech) — Roniewicz, p. 39–41, Pl. 6 figs. 2–4.

? 1989 *Distichophyllia norica* (Frech) — Stanley & Whalen, p. 806–807, fig. 5.4 and 5.6.

1989 Distichophyllia norica (Frech) — Stanley, p. 770.

1990 Distichophyllia norica (Frech) — Riedel, p. 61.

? 1990 *"Montlivaltia" verae* (Volz) — Riedel, Pl. 11 fig. 4.

1991 *Distichophyllia norica* (Frech) — Turnšek & Buser, p. 227, Pl. 2 figs. 4–5.

1991 Distichophyllia norica (Frech) — Riedel, p. 114.

? 1993 *Distichophyllum noricum* (Frech) — Liao & Xia, p.207, fig. 2-3.

? 1994 *Distichophyllia norica* (Frech) — Stanley, p. 88, Pl. 4 figs. 3–4.

1994 *Distichophyllia norica* (Frech) — Liao & Xia, p. 54, Pl. 2 figs. 8–12, Pl. 3 fig. 8.

1994 *Montlivaltia tenuise* Deng and Zhang — Liao & Xia, p161, Pl. 67 figs. 2, 4–6.

? 1995 *Distichophyllia norica* (Frech) — Prinz-Grimm, p. 235, fig. 3c.

1996 Distichophyllia norica (Frech) — Bernecker, p. 54.

1996 Distichophyllia norica (Frech) — Senowbari-Daryan, p. 302.

1997 *Distichophyllia norica* (Frech) — Turnšek, p. 79, fig. 79.

1997 *Distichophyllia gosaviensis* (Frech) — Turnšek, p. 78, fig. 78

2000 Distichophyllia cf. norica — Blodgett *et al.*, n° 9237

2001 *Distichophyllia norica* Frech — Melnikova, p. 46, Pl. 13 fig. 1.

2002 Distichophyllia cf. norica — McRoberts & Blodgett, p. 57.

2003 Distichophyllia norica (Frech) — Stanley & Yarnell, p 114.

2005 Distichophyllia norica (Frech) — Bernecker, p. 447 & 450.

2008 *Distichophyllia norica* (Frech) — Caruthers & Stanley, p.475, figs. 2.18–20, 2.25.

2009 Distichophyllia cf. norica (Frech) — Mannani & Yazdi, p. 368.

p 2010 *Distichophyllia norica* (Frech) — Rosenblatt, p. 99, Pl. 1 figs. 18–19, non Pl. 4 figs.15 & 19.

2012 *Distichophyllia norica* (Frech) — Shepherd *et al.*, p. 807, fig. 6–1–6–3, 6–6, 6–7, 6–10 and 6–11.

non 2013 *Distichophyllia norica* (Frech) — Liao & Deng, p. 42, Pl. 10 figs. 7–10, Pl. 11 figs. 1–6.

2013 *Distichophyllia norica xizangensis* Deng & Zhang — Liao & Deng, p. 39, Pl. 6 figs. 11–14.

2013 *Distichophyllia tenuise* (Deng & Zhang) — Liao & Deng, p. 42, Pl. 11 figs. 7–11.

2017 Distichophyllia norica (Frech) — Bo *et al.*, p. 272.

v. 2018 *Distichophyllia* sp. 2 — Vasseur, p.178-179, fig. 3.30.

v. 2019 *Distichophyllia norica* (Frech)— Boivin, p. 198, figs. 10.7 and 10.8.

? 2020 *Distichophyllia cf. norica* (Frech) — Mannani, p. 11, figs. 6-H and 6-I.

2020 *Cuifia elliptica* Melnikova — Mannani, p. 11, figs. 7-C —F.

v. 2021 *Distichophyllia norica* (Frech) — Vasseur & Lathuilière, p. 1244, fig. 40.

Type designation. Syntypes BSPG AS XII 46, 48, no lectotype designated.

Type locality and horizon. Norian — Rhaetian from Zlambach bei Aussee, Fischerwiese, Oedalm, Hammerkogel and Hallstätter Salzberg (Austria), and Scharitzkehl Alp (Germany).

Originally included material. The original type series included the specimen of Reuss (1854) and several hundred specimens collected by Frech (1890).

Etymology. From *norica* in Latin referring to the Noric Alps.

Material examined. 5 specimens: SB–55/5, SB–159, SB–165, SB–202 and SB–203 and 3 uncertain specimens: SB–138, SB–160/1 and SB–229.

Ages and localities of material examined. Upper Sinemurian from Serdrar reef and upper Sinemurian or lowermost Pliensbachian from Castle olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Solitary coral, corallum conical, transverse section of corallite circular to slightly elliptical. Radial elements are costosepta slightly bi-cuneiform or septa slightly attenuated, free, compact, wavy or zigzag. Septal apparatus is organised in 3 or 4 size orders. Septa of the first order are thick whereas septa of lower orders are thin. Lateral faces of septa are often ornamented by flattened, rounded or sharp granules. Inner margins of septa are rounded, slightly pointed or club-shaped, often reaching the centre of the corallite producing a parietal columella. The fossa is straight and elongated. General symmetry is hexameral and slightly bilateral due to the elongation of the fossa. Endotheca is made of large vesicular dissepiments regularly distributed in the interseptal space. Wall perhaps parathecal.

Dimensions. Calicular great diameter 10.5 to 30.5 mm — Calicular small diameter 14 to 24.5 mm — Number of septa 55 to 90 septa — Septal density 3 to 9 septa per 2 mm.

Similarities and differences. *Distichophyllia norica* differs from:

— *Distichophyllia fritschi* (Frech, 1890) that has strong protruding granulations of the lateral faces of its septa.

— *Distichophyllia major* (Roniewicz, 1996) that has a larger calice (between 35 to 50 mm), a denser septal apparatus (9 to 12 septa per 1 mm) and a higher length of S3 septa.

— *Distichophyllia melnikovae* (Montanaro Gallitelli, 1975) that has thicker septa. In the initial description, the distinction with *D. norica* is based on thickness of septa and number of septa (60 septa for *D. melnikovae* instead of 200 for *D. norica* according to Montanaro Gallitelli, Russo, and Ferrari, 1979). However, this low number appears included in the intra-specific variability of *D. norica*. It is possibly a junior synonym.

— *Distichophyllia tabulata* (Roniewicz, 1996) that has a larger calice (between 40 to 65 mm), tabuloid dissepiments and fusiform septa.

Stratigraphic and geographic distribution. Upper Triassic from China, Russia, Tibet, Carnian from Japan, Carnian – Norian from China and USA, Norian from Bosnia and Herzegovina, Canada, China, Iran, Oman, Peru, Romania, Russia and USA (including Alaska), Norian — Rhaetian from Austria, Chile, Iran, Tajikistan, Slovenia and Timor, Sinemurian – Pliensbachian from Morocco (High Atlas Mountains).

Genus ***Retiophyllia*** (Cuif, 1966)

Type species. *Retiophyllia frechi* (Roniewicz, 1989) nomen novum pro *Thecosmilia fenestrata* (Reuss, 1854) *in* (Frech, 1890) (p. 9, Pl. 1 figs. 25–27, Pl. 2 figs. 1–11 & 13–17 non 12) non *Calamophyllia fenestrata* (Reuss, 1854) (p. 105, Pl. 5 figs. 20–21). The type species was not properly designated in Cuif (1966: p. 130). The designation was corrected in Roniewicz (1989).

Originally included species. Only the type species.

Similarities and differences. The genus *Retiophyllia* (Cuif, 1966) differs from the phaceloid genera by its distichophylliid structure and its typical epitheca. This genus remains difficult to distinguish from *Paracuifia* (Melnikova, 2001) and *Paravolzeia* (Roniewicz *et al.*, 2005). The shape of septa, the existence of costae, and remains of the mid septal zigzag line mostly guide the attribution. *Thecactinastraea*

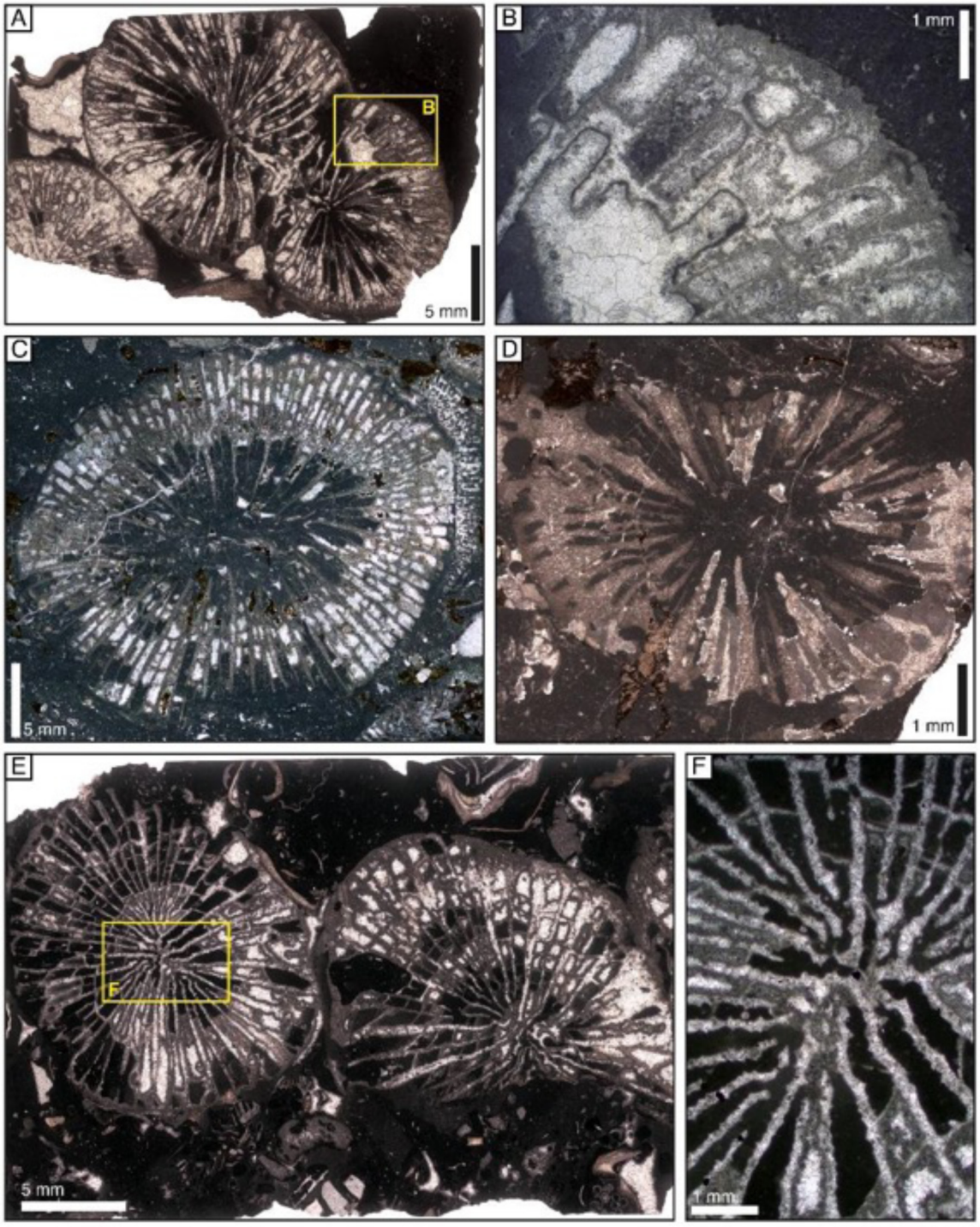

Fig. 22. *Distichophyllia norica* (Frech, 1890). A Transverse thin section of three contiguous corallites (specimens SB–202). B Enlargement of A. C Transverse thin section of the specimen SB–159. D Transverse thin section of the specimen SB–165. E Transverse thin section of the specimen SB–203. F Enlargement of E.

(Beauvais, 1986) has much more ornamented septa and *Phacelostylophyllum* (Melnikova, 1972) is stylophyllid in septal structure.

Etymology. Probably from the Rhaetian age and *phyllia*: leaf in ancient Greek.

Status. Available and valid.

Retiophyllia*? *cf. gracilis (Roniewicz, 1989)
Figure 23

* 1989 *Retiophyllia gracilis* sp. nov. — Roniewicz, p. 58–59, Pl. 9 fig. 9, Pl. 10 fig. 2, Pl. 13 fig. 3.

1998 *Retiophyllia gracilis* Roniewicz — Roniewicz & Michalik, p. 396, fig. 1.1.

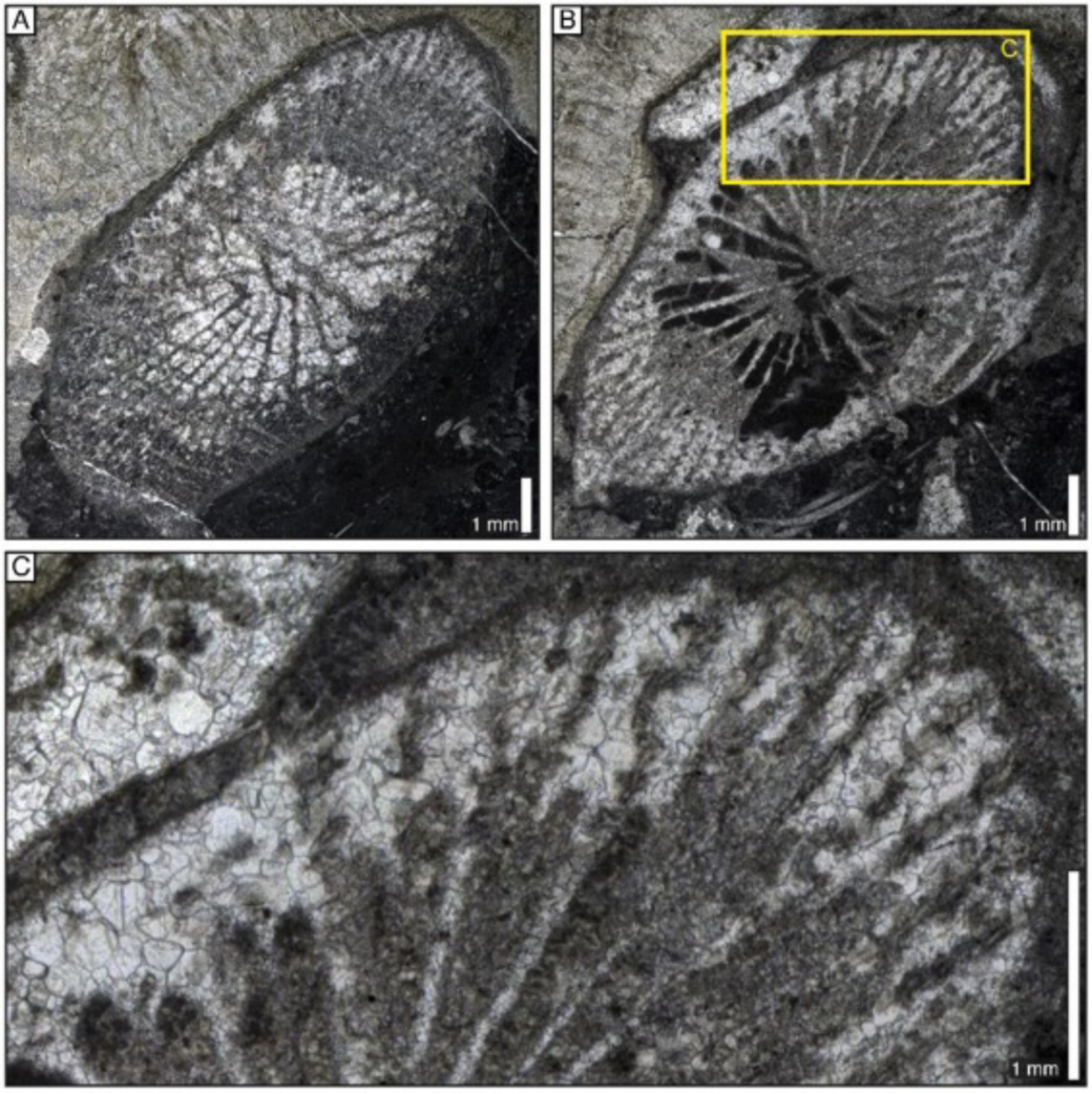

Fig. 23. *Retiophyllia*? *cf. gracilis* (Roniewicz, 1989). A–B Transverse thin sections of two branches of the specimen SB–204/2. C. Enlargement of B.

v 2009 *Retiophyllia? cf. gracilis* Roniewicz — Boivin, p. 256–257, fig. 10.32.

Type designation. Holotype by original designation, NHMW 1982/56/9.

Type locality and horizon. Norian — Rhaetian from Kesselwand-Rohrmoos, Zlambach Beds, Northern Calcareous Alps, Austria.

Originally included material. Several colonies and isolated corallites from Fischerwiese and Kesselwand-Rohrmoos, 8 thin sections.

Etymology. From *gracilis*: slim in Latin referring to the narrow corallite diameters.

Material examined. 1 specimen: SB–204/2.

Ages and localities of material. Upper Sinemurian from Serdrar reef, Amellagou Region, High Atlas Mountains, Morocco.

Description. Phaceloid colony. Radial elements are costosepta (Fig. 23C), compact, free, thin, straight, occasionally in zigzag. Septal apparatus organised in three size orders hierarchized in length but not in thickness. S1 septa reach the centre of calice. S2 septa measure circa three quarter of the radius of the calice. S3 are short. Lateral faces of septa are ornamented with sharp granules. The inner margin of S1 septa is slightly enlarged. Columella perhaps parietal. Endotheca made of thin dissepiments. The structure of the wall is not well preserved and remains difficult to decipher.

Dimensions. Diameter of branches circa 3.7 to 5.5 mm — Number of septa circa 40 septa — Septal density 6 septa per 2 mm — Distance between trabecular axes 120 to 200 µm.

Remarks. This specimen is referred to *Retiophyllia gracilis* (Roniewicz, 1989) based on its diameter, thickness and number of septa, and the organisation of size orders. However, distinctions between species of *Retiophyllia* are based mainly on the morphology of dissepiments, microstructure and dimensions (see (Roniewicz, 1989), Tab. 2 p. 44). In

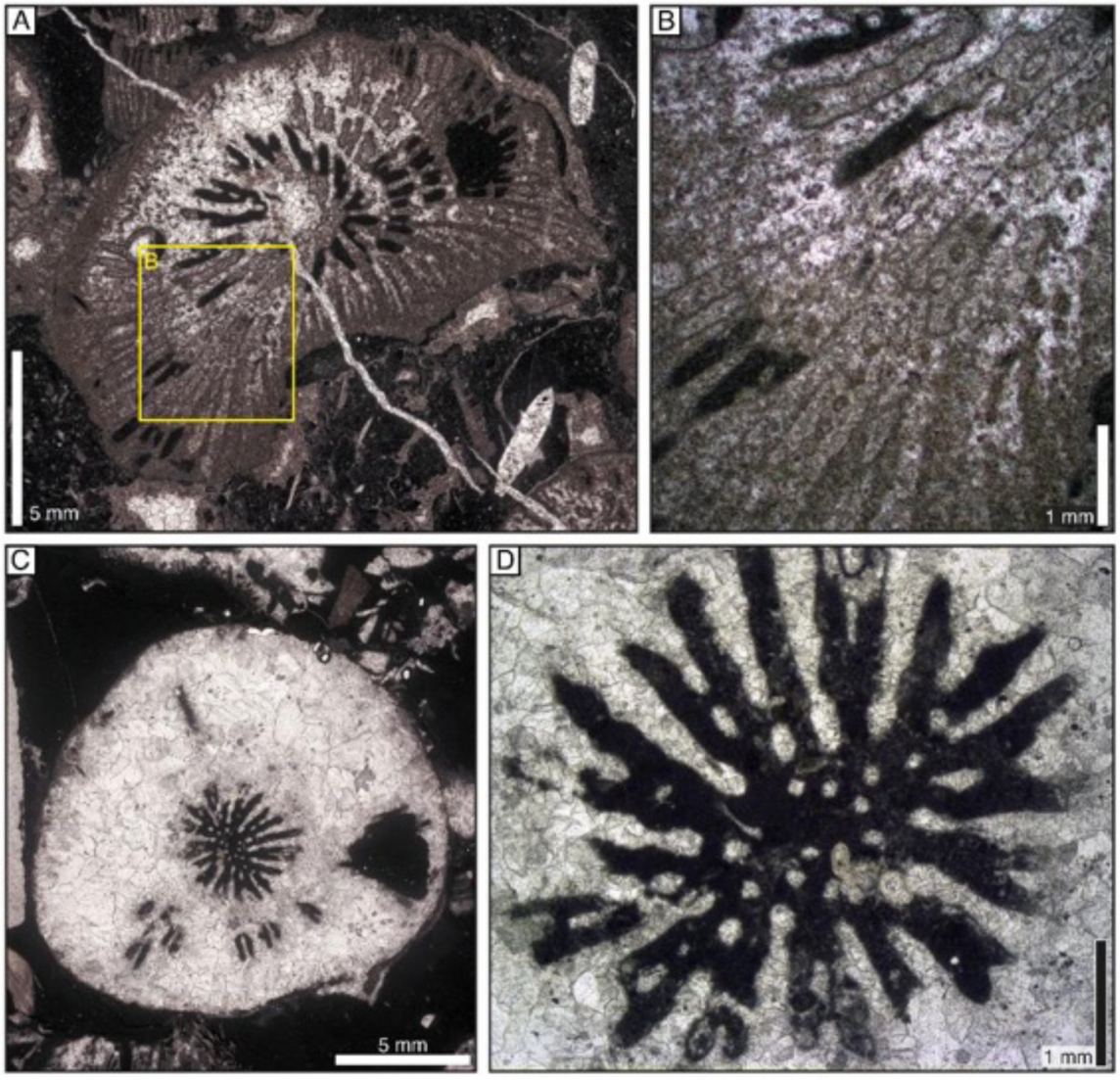

Fig. 24. *Epismiliopsis* sp. A Transverse thin section of the specimen SB–55/2. B Enlargement of A. C Transverse thin section of the specimen SB–331. D Enlargement of C.

the lack of longitudinal section, it is impossible to confirm the identification.

Stratigraphic and geographic distribution. Rhaetian of Austria (Northern Calcareous Alps) and Slovakia (Western Carpathians) — Sinemurian from Morocco (High Atlas Mountains).

Family **Stylophyllidae** (Frech, 1890)

Genus ***Epismiliopsis*** (Alloiteau, 1952)

Type species. *Epismilia liasica* (Fromentel and Ferry, 1865b): p. 53, Pl. 15 fig. 3 by monotypy.

Originally included species. Only the type species.

Similarities and differences. The genus *Epismiliopsis* is very close to *Stylophyllopsis* Frech, 1890, even possibly congeneric, but differs by its elongated fossa and the torsion of its lateral septa. For other solitary genera, see *Stylophyllopsis*.

Etymology. From the genus *Epismilia* and *opsis*: appearance of in ancient Greek, referring to the similarity with the genus *Epismilia*.

Status. Available and valid.

***Epismiliopsis* sp.**

Figure 24

v p 2019 *Stylophyllopsis?* sp. — Boivin, p. 258, fig. 10.33.C–D, non fig. 10.33.A–B.

Material examined. 1 specimen: SB–331.

Ages and localities of material. Upper Sinemurian from Serdrar reef, Amellagou Region, High Atlas Mountains, Morocco.

Description. Solitary coral, conical corallum, transverse section of the corallite sub-circular. Septa with stylophyllid structure, free or sometimes joined. Septal apparatus organised in three or four size orders. Lateral septa of the first order are slightly bent. Inner margin of septa characterised by dissociated free septal spines, which are projected in the lumen. Septal spines are themselves ornamented according to the star-shape pattern described by Stolarski and Russo (2002, see Figs. 5 and 7). Fossa elongated. Endotheca made of dissepiments.

Dimensions. Calicular diameter 15 mm — Number of septa circa 60 septa (approximated).

Similarities and differences. We have compared our specimen to the nominal species of *Epismiliopsis*. Among them, *E. conica* (Beauvais, 1967) appears to be a Bajocian *Montlivaltia*. Four other nominal species are known: *E. eudesi* (Fromentel and Ferry, 1865b), *E. liasicus* (Fromentel and Ferry, 1865b), *E. densserrae* (Fromentel and Ferry, 1867), *E. pareudesi* (Vasseur and Lathuilière, 2021). The three latter species have too large dimensions in comparison to our specimen, which is close to *E. eudesi* but with a higher number of septa. However, *E. eudesi* is known by a single specimen, which could be a young corallum of *E. pareudesi*, as already noted by Vasseur and Lathuilière (2021). Accordingly, our specimen could also be a young corallum. Considering that it is also imperfectly preserved, we keep it in open nomenclature.

From the observation of the original figures (Terquem and Piette, 1865 Pl. 16 figs. 17–21), we cannot exclude an assignment to *Epismiliopsis* of *Montlivaltia polymorpha* (Terquem and Piette, 1865) because of the torsion of septa, and the elongation of the fossa.

Stratigraphic and geographic distribution. Sinemurian from Morocco (High Atlas Mountains).

Genus ***Lepidophyllia*** (Duncan, 1868)

Type species. *Lepidophyllia hebridensis* (Duncan, 1868) by subsequent designation (Wells, 1936): p. 114.

Originally included species. *Lepidophyllia hebridensis* (Duncan, 1868) and *Lepidophyllia stricklandi* (Duncan, 1868).

Etymology. From *lepidos*: blade and *phyllia*: leaf in ancient Greek.

Status. Available and valid.

Subgenus *Heterastraea* (Tomes, 1888

Type species. *Isastræa tomesii* (Duncan, 1868) by subsequent designation (Vaughan and Wells, 1943): p.156.

Originally included species. *Isastræa murchisoni* Wright in (Duncan, 1867), *Septastræa eveshami* (Duncan, 1868), *Septastræa fromenteli* (Terquem and Piette, 1865), *Isastræa stricklandi* (Duncan, 1868), *Isastræa insignis* (Duncan, 1868), *Isastræa endothecata* (Duncan, 1868), *Septastræa haimei* Wright in (Duncan, 1867), *Isastræa tomesii* Duncan, 1868), *Isastræa latimœandroidea* (Duncan, 1868), *Septastræa excavata* Fromentel in (Martin, 1860), *Heterastræa etheridgei* (Tomes, 1888), *Heterastræa regularis* (Tomes, 1888), *Heterastræa bintonensis* (Tomes, 1888) and *Heterastræa* sp. (Tomes, 1888). The species *Isastræa sinemuriensis* Fromentel in Martin, 1860) was included with doubt.

Similarities and differences. The subgenus *Lepidophyllia* (*Heterastraea*) differs from other cerioid taxa:

- *Lepidophyllia (Lepidophyllia)* Duncan, 1868) that is bifacial and has numerous rejuvenescences (Gretz *et al.*, 2013).
- *Rhaetiastraea* (Roniewicz, 1974) by the non-trabecular nature of its septa (or at least the quasi exclusive proportion of thickening deposits in their microstructure), which implies a very limited ornamentation of lateral faces of septa. Moreover, no mid-wall line was described in *Rhaetiastraea*.
- *Latiastrea* (Beauvais, 1964), that has septa with pennular structure and endotheca made by vesicular dissepiments.
- *Hispaniastraea* (Turnšek and Geyer, 1975), that has a characteristic major septum.
- *Chondrocoenia* (Roniewicz, 1989), that is an actinastreid easily distinguished by its columella.
- *Isastrea* (Edwards and Haime, 1851b) that has a montlivaltid septal structure with carinae and a very different wall made of various components.

Etymology. From *heteros:* other in ancient Greek, probably referring to the other true *Isastrea*.

Status. Available and valid.

Lepidophyllia (Heterastraea) microcalix sp. nov.

Figures 25–27

v. 2019 *Lepidophyllia (Heterastraea) microcalix* (unavailable name, ICZN art. 8.3) — Boivin: p. 216, figs. 10.16, 10.17 and 10.18. 3.

Type designation. Holotype SB-220 (Fig. 26-D) and 30 paratypes: SB–48, SB–55/1, SB–57, SB–154, SB–193 (silicified), SB–196, SB–197, SB– 204/1, SB–210/1, SB–211, SB–212, SB–213, SB–216, SB–218/1, SB–224/1, SB–227, SB–228, SB–230/2, SB–250, SB–318/1, SB–319, SB–320, SB–321/1, SB–322, SB–325, SB–327, SB–329, SB–330, SB–333 and SB–340.

Type locality and horizon. Upper Sinemurian from Serdrar reef (sampling spot 2: N 32.00788° W 4.94478°), Amellagou Region, High Atlas Mountains, Morocco.

Ages and localities of paratypes. Dromedary biostrome (Hettangian or Sinemurian), Upper Sinemurian from Serdrar reef, Upper Sinemurian or lowermost Pliensbachian from Castle olistolith and Lower Pliensbachian from Owl olistolith — Amellagou Region, High Atlas Mountains, Morocco.

Etymology. From *micro*: small in ancient Greek and *calix* in Latin or *kulix* in ancient Greek: calyx, cup, referring to the small dimension of the calices.

Diagnosis. *Lepidophyllia (Heterastraea)* with small calices (see Tab. 5).

Description. Colonies cerioid. Corallites polygonal. Septal intracalicular budding (Figs 25–25, 26–E-F). Septa compact except the inner margin, free or sometimes joined (including contratingent junctions), confluent or not confluent, curved or wavy. Septal apparatus organised in three size orders, regularly hierarchized in length and thickness. Lateral faces of septa ornamented by fine granules. Spines are dissociated at inner margin of septa, orientation sub-horizontal of free spines (Fig. 26–A). The axial space is occupied by free spines. Depending on the length of septa and the depth of the transverse section, the axial region can be (1) a large fossa (Fig. 25–E), (2) occupied by a papillose columella made of free spines (Fig. 25–B) or (3) occupied by a parietal columella made of junction of septa (Fig. 26–E-F). No pali. Endotheca made of thin wide dissepiments occasionally steeply inclined (Fig. 26–A). Wall septothecal? Mid-wall line sometimes visible (Figs. 25–25–25, 26–E–F).

Dimensions. Dimensions are given in Table 5. The species present a moderate variability of the great and small diameters, the distance from corallite to corallite and the number of septa. The distribution of these dimensions is continuous (Fig. 27–A) and the morphospace is homogeneous (Fig. 27–B). The thickness of the wall and the septal density are still less variable. Consequently, we have no reason to split this species into several units.

Similarities and differences. *Lepidophyllia* (*Heterastraea*) *microcalix* has the smallest calices among nominal species of *Lepidophyllia* (*Heterastraea*) described in the

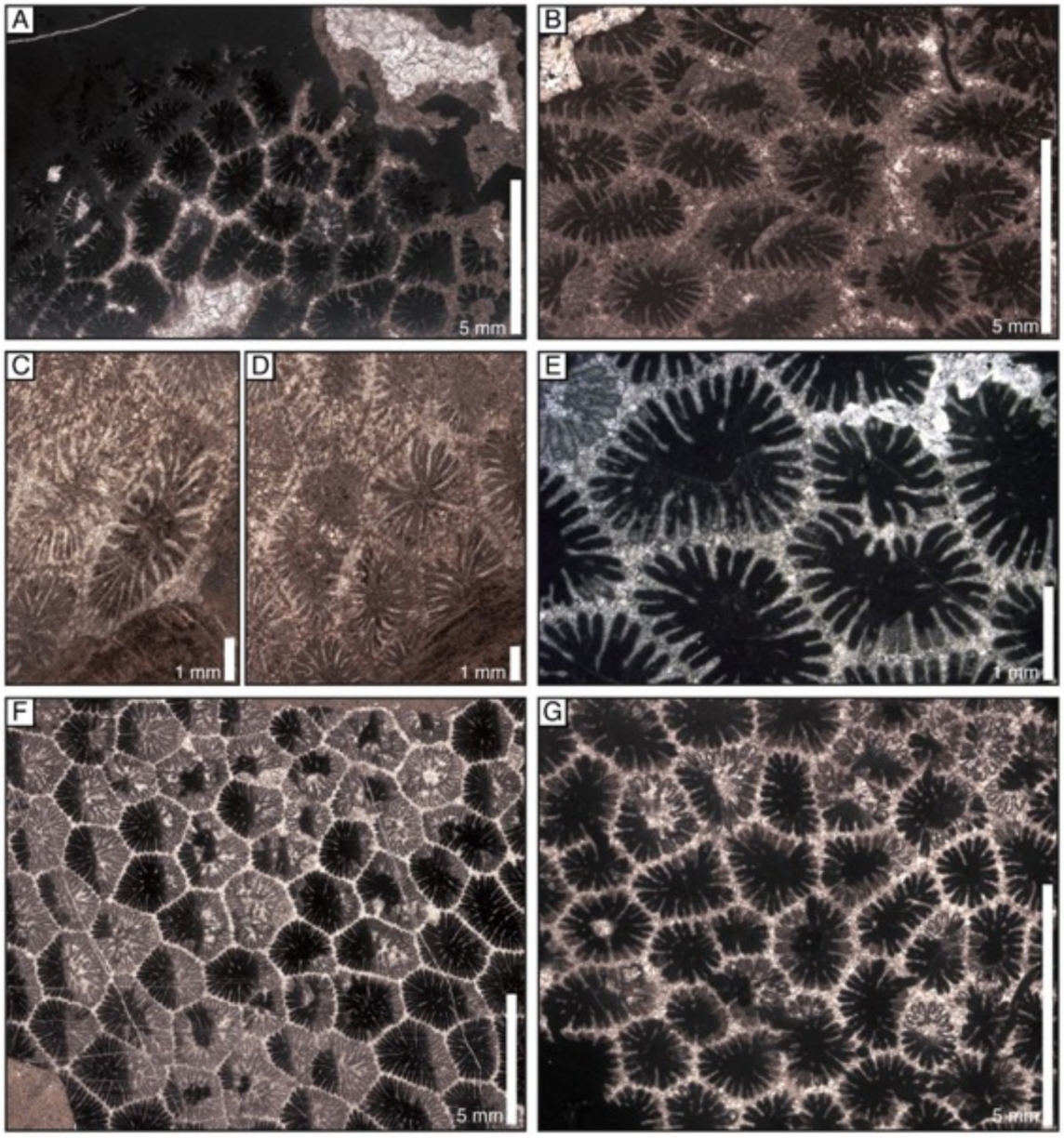

Fig. 25. *Lepidophyllia (Heterastraea) microcalix* sp. nov. A Transverse section of the colony SB–48. B Transverse section of the colony SB–204/1. C–D Transverse sections of the colony SB–210/1. G Transverse section of the colony SB–329. F Transverse section of the colony SB–211. G transverse section of the colony SB–318/1.

literature (Tab. 6, Figs. 28 and 29): its diameter, distance from corallite to corallite and its number of septa are the smallest. Moreover, its septal density is higher than other species, except *L.* (*H.*) *angelae*. The PCA on the nominal species dimensions (Fig. 29) shows a clear separation between *L. (H.) microcalix* and other species on the second principal component (29.9% of total variance).

Stratigraphic and geographic distribution. Hettangian? – Sinemurian – lower Pliensbachian from Morocco (High Atlas Mountains).

Genus ***Phacelostylophyllum*** (Melnikova, 1972)

Type species. *Stylophyllopsis zitteli* (Frech, 1890), p. 49, Pl. 13 figs. 9–15 & 17–24 by original designation.

Originally included species. *Phacelostylophyllum*? *pontebbanae* (Volz, 1896), *Phacelostylophyllum romerloana* (Volz, 1896), *Phacelostylophyllum caespitosa* (Frech, 1890), *Phacelostylophyllum pygmaeum* (Frech, 1890), *Phacelostylophyllum zitteli* (Frech, 1890), *Phacelostylophyllum karauldyndalaensis* (Melnikova, 1972).

Remarks. Here, *Phacelostylophyllum* has been described separately as a morphogenus defined by its phaceloid character but phyletically very close to *Stylophyllopsis* (Frech, 1890). That is why we choose to write *Phacelostylophyllum* mg. in conformity with the spectral nomenclature (Lathuilière, 1996).

Similarities and differences. The genus *Phacelostylophyllum*, stylophyllid in structure, differs from the phaceloid genera:

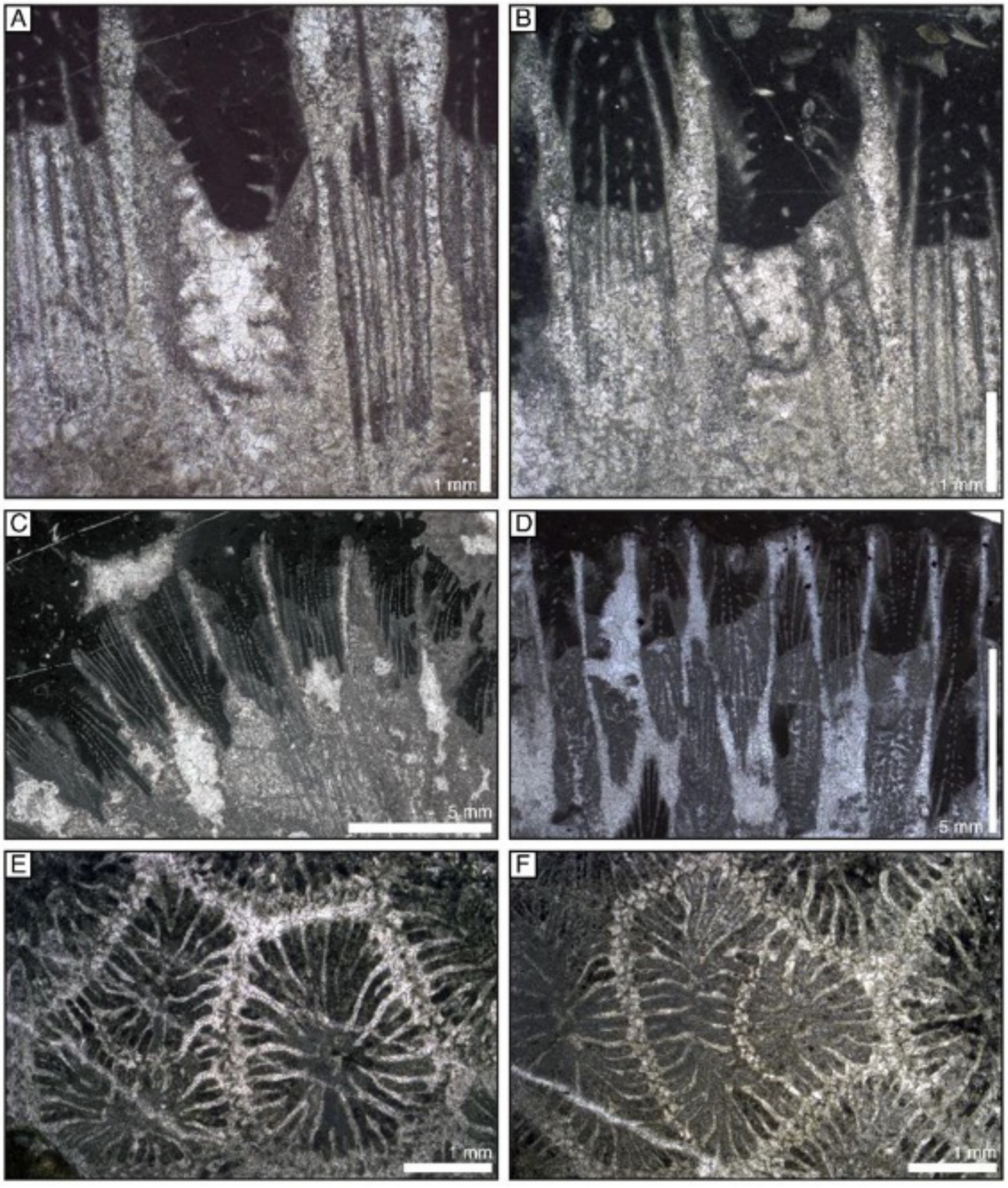

Fig. 26. *Lepidophyllia (Heterastraea) microcalix* sp. nov. A–B longitudinal sections of the colony SB–329. Note the two opposite septa cut longitudinally in the centre of the corallite and the ornamentation of their inner margins (A). C longitudinal section of the colony SB–228. D longitudinal section of the holotype SB–220. E–F transverse sections of the colony SB–216, note the septal intracalicular budding.

- *Lochmaeosmilia* (Wells, 1943) that shows typical apophyses.

- *Paracuifia* (Melnikova, 2001) and *Paravolzeia* (Roniewicz *et al.*, 2005) which also have poorly ornamented septa, but do not show detachment of the septal spines at the distal inner edge.

- *Thecactinastraea* (Beauvais, 1986) that has much more ornamented septa.

- *Pinacophyllum* (Frech, 1890) that has complete tabulae.

- *Retiophyllia* (Cuif, 1966) that is a distichophyllid in structure and shows a typical epitheca.

Etymology. From *phacelos:* fascicle in ancient Greek and *−stylophyllum* referring to the genus *Stylophyllum* (Frech, 1890).

Status. Available and valid.

Phacelostylophyllum* mg. *martini (Fromentel, 1860) Figure 30

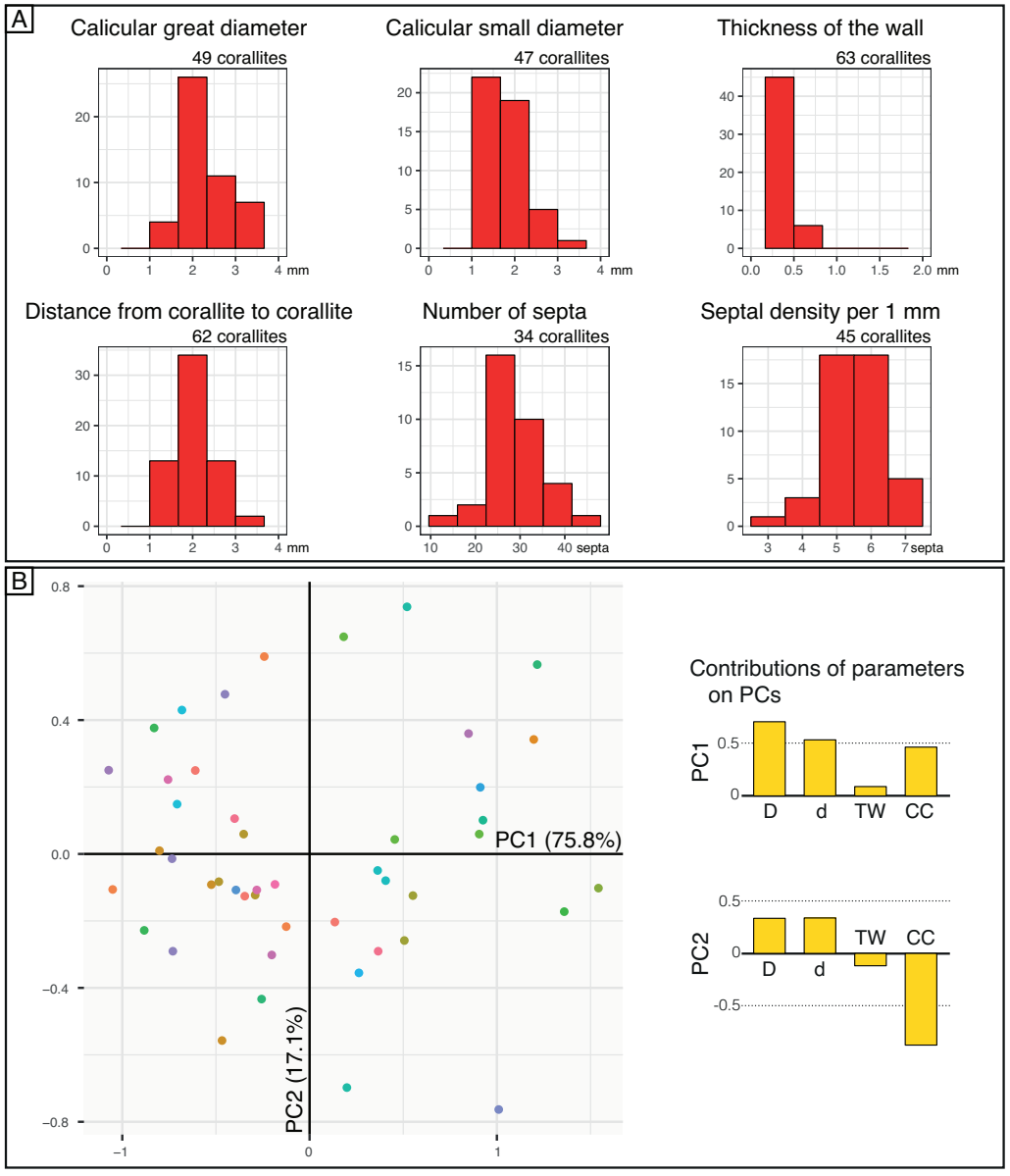

Fig. 27. Plots of morphometrical measurements of *Lepidophyllia (Heterastraea) microcalix* sp. nov. A Histograms of morphometrical measurements (calicular great diameter, calicular small diameter, thickness of the wall, distance from corallite to corallite, number of septa and septal density). B Morphospace plot of corallites from studied colonies computed with PCA (co-variance matrix) on the two calicular diameters (great and small), thickness of the wall and distance from corallite to corallite. Each dot color represents one colony. The two first principal components explain 92.9% of the total variance.

Table 5. Dimensions of *Lepidophyllia* (*Heterastraea*) *microcalix* sp. nov. specimens.

Measure	Minimum	Median	Maximum	Mean	St. dev.	Dimensions of holotype
Calicular great diameter (mm)	1.40	2.19	3.87	2.30	0.58	1.75 – 2.61
Calicular small diameter (mm)	1.26	1.73	3.40	1.85	0.47	2.09 – 2.63
Thickness of the wall (mm)	0.10	0.21	0.71	0.27	0.14	0.13 – 0.21
Distance from corallite to corallite (mm)	1.32	2.06	3.46	2.09	0.46	1.67 – 2.77
Number of septa (septa)	14	28	46	28.88	6.38	40
Septal density (septa per 1 mm)	3	6	7	5.51	0.87	5 – 7

Table 6. Comparisons between dimensions of *Lepidophyllia* (*Heterastraea*) nominal species. Two first measurements are in millimetres and rounded to the nearest half-millimetre. D diameter, CC distance from calice to calice, NS number of septa, Sd septal density. The dimensions are those from: 1 Beauvais (1976), 2 Turnšek and Kosir (2000), 3 Turnšek, Buser, and Debeljak (2003), 4 Gretz (2014), 5 Tomes (1888), 6 Terquem and Piette (1865), 7 Fromentel (1860).

Nominal species	D	Cc	Ns	Sd	References
L. (H.) angelae	3–10	3 – 10	96 – 150	15 – 18 s./2 mm	3
L. (H.) bintonensis	4 – 5	?	40 – 46	?	5
L. (H.) endothecata	2.5 – 13	3.5 – 7	33 – 75	3-6 s./2 mm	1 & 4
L. (H.) etheridgei	3 – 6	3 – 4.5	26 – 32	4 – 5 s./2 mm	4
L. (H.) eveshami	2 – 8	4 – 6	18 – 48	3 – 6 s./2 mm	1, 2 & 4
L. (H.) excavata	3.5 – 8.5	3 – 8.5	32 – 46	3 – 5 s./2 mm	1 & 4
L. (H.) fromenteli	7–15	?	24 – 52	?	6
L. (H.) haimei	4.5 – 8.5	3.5 – 5	34 – 44	3 – 6 s./2 mm	4
L. (H.) latimaeandroidea	4 – 9.5	?	45 – 70	6 s./2 mm	1
***L. (H.) microcalix* sp. nov.**	**1.5 – 4**	**1.5 – 3.5**	**14 – 46**	**4 – 7 s/1 mm**	**this work**
L. (H.) morencyana	2.5 – 9	2 – 5.5	17 – 32	2 – 5 s./2 mm	4
L. (H.) insignis	3.5 – 12.5	3.5 – 5.5	29 – 65	3 – 5 s./2 mm	1 & 4
L. (H.) regularis	4.5 – 7	4 – 5	28 – 36	3 – 4 s./2 mm	4
L. (H.) sinemuriensis	6 – 8	?	$\leq$ 78	?	7
L. (H.) stricklandi	3 – 10	3 – 7	30 – 55	3 – 6 s./2 mm	1, 2 & 4
L. (H.) tomesi	2.5 – 10	3 – 8	28 – 48	3 – 6 s./2 mm	1, 3 & 4

v* 1860 *Thecosmilia martini* sp. nov. — Fromentel *in* Martin, p. 92, Pl. 8 fig. 8–9.

1861 Thecosmilia martini Fromentel — Fromentel, p. 142.

1864 *Thecosmilia martini* Fromentel — Dumortier, p. 95, Pl. 15 figs. 4, 6, 7.

1865 *Thecosmilia martini* Fromentel — Terquem & Piette, p. 127, Pl. 17 figs. 1–3.

1868 *Thecosmilia martini* Fromentel — Duncan, p. 45, Pl. 12 fig. 1–2.

1878 Thecosmilia martini Fromentel — Tomes, p. 186.

1884 *Thecosmilia martini* Fromentel — Koby, p. 164, Pl. 54 fig. 5.

1894 *Thecosmilia martini* Fromentel — Koby, p. 16, Pl. 4 fig. 3.

1936 Thecosmilia martini Fromentel — Joly, p. 170

? 1991 *Phacelostylophyllum suttonensis* (Duncan) — Prinz, p. 160–161, Pl. 1 fig. 10.

v. 2014 *Phacelostylophyllum martini* (Fromentel) — Gretz, p. 73, Pl. VI fig. e–f.

v. 2018 *Phacelostylophyllum ?suttonensis* (Duncan) — Boivin *et al.*, fig. 3–e-g.

v. 2018 *Phacelostylophyllum* sp. 1 — Vasseur, p. 286, fig. 3.74.

v. 2019 *Phacelostylophyllum martini* — Boivin, p. 248, fig. 10.28.

v. 2021 *Phacelostylophyllum* mg. *martini* — Vasseur & Lathuilière, p. 1258, fig. 50.

Type designation. Holotype by monotypy. MHNG GEPI 36077.

Type locality and horizon. Sinemurian from Semur-en-Auxois, Burgundy, France.

Originally included material. Only the holotype.

Etymology. Dedicated to Jules Martin.

Material examined. 2 colonies: SB–205 and SB–231.

Ages and localities of material. Upper Sinemurian from Serdrar reef, Amellagou Region, High Atlas Mountains, Morocco.

Description. Colonies phaceloid. Transverse section of branches sub-circular. Radial elements are sub-compact, free, straight septa. Costae not observed. Septal apparatus organised in three size orders hierarchized in length. S1 septa are long and reach the axial region with perhaps projections. S2 septa measure circa a half of the radius. S3 are very short. Structure of septa perhaps stylophyllid, difficult to confirm due to the preservation. Lonsdaleoid septa. Endotheca made of large vesicular to tabular dissepiments (Fig. 30B). Wall nature unknown.

Dimensions. Diameter of branches 12 to 19 mm — Septal density 2 to 4 septa per 2 mm. — Endothecal density 2 to 3 dissepiments per 5 mm.

Similarities and differences. *Phacelostylophyllum martini* (Fromentel, 1860) differs from *Phacelostylophyllum suttonensis* (Duncan, 1867) that presents smaller calices (lower than 10 mm in diameter).

Stratigraphic and geographic distribution. Lower Jurassic from Western Europe, Hettangian from Scotland, Sinemurian from France (Languedoc) and Morocco (High Atlas Mountains), Pliensbachian from France (Pyrenees Mountains).

Phacelostylophyllum* mg. *suttonensis (Duncan, 1867) Figure 31

* 1867 *Thecosmilia suttonensis* sp. nov. — Duncan, p. 11-12, Pl. IV figs. 7–9.

1884b *Thecosmilia suttonensis* Duncan — Tomes, p. 365.

non 1911 *Calamophyllia suttonensis* sp. nov. — Clapp & Shimer, p. 431, Pl. 40 figs. 5 and 7, Pl. 41 fig. 15.

1976 *Phacelepismilia suttonensis* (Duncan) — Beauvais, p. 68-69, Pl. XV fig. 1, text-fig. 34.

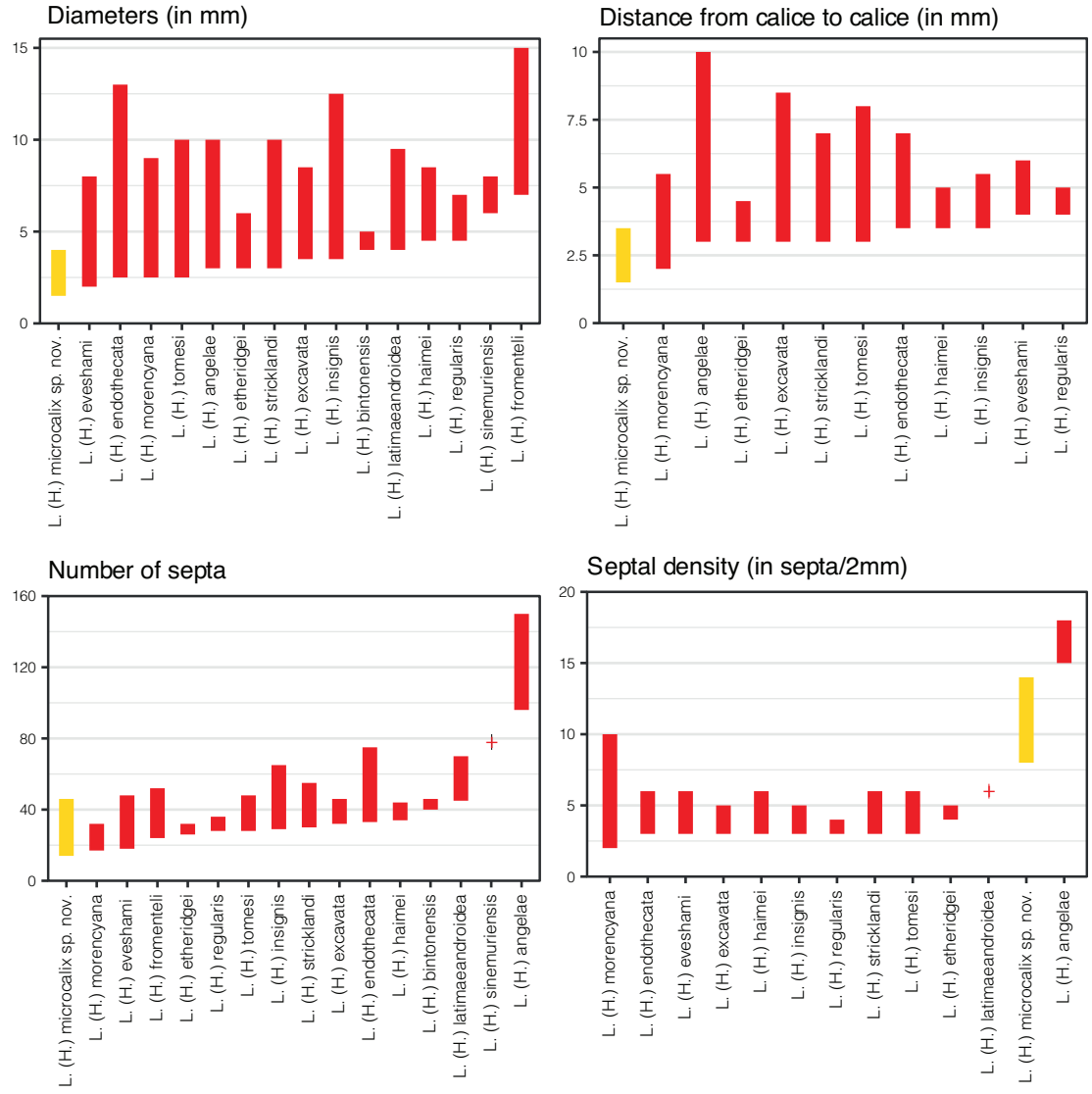

Fig. 28. Plot of dimensions for *Lepidophyllia* (*Heterastraea*) nominal species presented in Table 6.

1983 Phacelepismilia suttonensis (Duncan) — Negus, p. 253.

non 1986 *Thecactinastraea fasciculata* sp. nov. — Beauvais, p. 33, Pl. 5 fig. 1, text-fig. 21.

non 1979 "*Thecosmilia*" *cf. suttonensis* (Clapp & Shimer) – Stanley, p. 34, Pl. 3 fig. 2.

non 1989 *Retiophyllia suttonensis* (Clapp & Shimer) – Stanley, p. 770, figs. 5–6.

1991 Phacelepismilia suttonensis (Duncan) — Negus, p. 255, Table 1

2002 *Phacelepismilia suttonensis* (Duncan) — Simms, Little, & Rosen, p. 34, figs. 6–7.

non 2009 *Phacelophyllia suttonensis* (Duncan) — Kiessling *et al.*, p. 665, figs. 4D, 7F, 9A–C.

? 2009 *Phacelostylophyllum cf. michelini* (Terquem and Piette) — Kiessling *et al.*, p. 666, fig. 9–f-g.

v. 2014 *Phacelostylophyllum suttonensis* (Duncan) — Gretz, p. 103–104, Pl. 9.

v non 2018 *Phacelostylophyllum* ?*suttonensis* (Duncan) — Boivin *et al.*, fig. 3–e-g.

v. 2019 *Phacelostylophyllum suttonensis* (Duncan) — Boivin, p. 250–251, fig. 10.29.

Remarks. *Phacelophyllia suttonensis* (Duncan) *in* Kiessling *et al.* (2009) is interpreted as a heterogenous assemblage of *Heterastraea* (Fig. 9.A–C) and a true *Phacelophyllia* (Fig. 7.F); the latter considered a junior synonym of *Thecactinastraea* according to Melnikova and Roniewicz (2017). The status of the type specimen of *Thecosmilia suttonensis* Duncan is still disputable and has been successively attributed to *Thecosmilia, Phacelepismilia, Phacelophyllia* and *Phacelostylophyllum*. Obviously, this species cannot remain in its original genus because of the montlivaltiid structure of *Thecosmilia*. *Phacelepismilia* has been considered a synonym of *Archaeosmiliopsis* a genus with compact septa without spines (Kiessling *et al.*, 2009). In addition, the type specimen of the type species (*Montlivaltia simplex* Duncan) of *Phacelepismilia* is not clearly phaceloid. The generic attribution of *Thecosmilia suttonensis* Duncan to *Thecactinastraea* or *Phacelostylophyllum* is more difficult, especially because of the unavailability of thin sections. Based

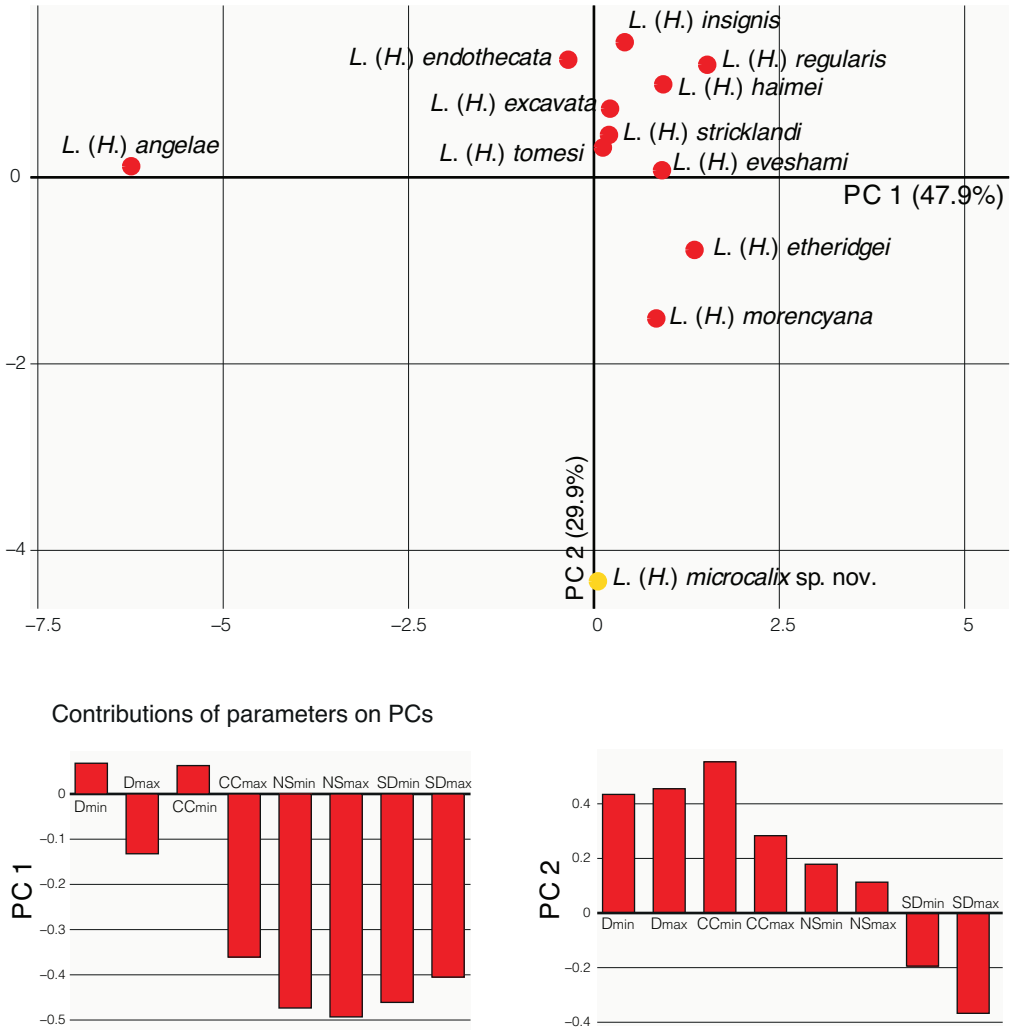

Fig. 29. Morphospace plot of *Lepidophyllia* (*Heterastraea*) nominal species computed with PCA (co-variance matrix) on the dimensions from litterature presented in Table 6: calicular diameters (Dmin minimum value and Dmax maximum value), distance from corallite to corallite (CCmin minimum value and CCmax maximum value), number of septa (NSmin minimum value and NSmax maximum value) and septal density (SDmin minimum value and SDmax maximum value). The two first principal components explain 77.8% of total variance.

on the literature (Duncan, 1867; Beauvais, 1976) and in the absence of direct observation of the type specimen, we assigned this species to *Phacelostylophyllum* because of the apparent weak ornamentation of septa and the probable development of tabuloid dissepiments.

Type designation. Holotype by monotypy. Collection Moore BRLSI 288.

Type locality and horizon. Hettangian, Angulata chronozone, from Sutton Stone, Wales, Great Britain.

Originally included material. Only the holotype.

Etymology. From *sutton* referring to the type locality.

Material examined. 1 colony: SB–170 and 3 uncertain silicified colonies: SB–39, SB–87 and SB–192.

Ages and localities of material examined. ?Hettangian–Sinemurian from Dromedary biostrome and upper Sinemurian or lowermost Pliensbachian from Castle olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Colonies phaceloid. Transverse section of branches sub-circular. Radial elements are septa, costae not observed, sub-compact, free, straight. Septal apparatus organised in two or three size orders hierarchized in length. S1 septa are long, reach the axial region and show projections inducing a weak papillose columella. Structure of septa perhaps stylophyllid, difficult to confirm due to the preservation. Endotheca made of large vesicular to tabular dissepiments (Fig. 31B). Wall nature unknown.

Dimensions. Calicular diameter 2.1 to 7.5 mm — Septal density 4 septa per 2 mm.

Similarities and differences. *Phacelostylophyllum suttonensis* (Duncan, 1867) differs from *Phacelostylophyllum martini* (Fromentel, 1860) which has larger calices (between 10 and 20 mm diameter). *Phacelostylophyllum suttonensis* (Duncan, 1867) is very close of *Phacelostylophyllum michelini* (Terquem and Piette, 1865) but the latter does not show detachments in the axial region.

Stratigraphic and geographic distribution. Hettangian from Wales, Sinemurian from France, Sinemurian – early Pliensbachian from Morocco (High Atlas Mountains).

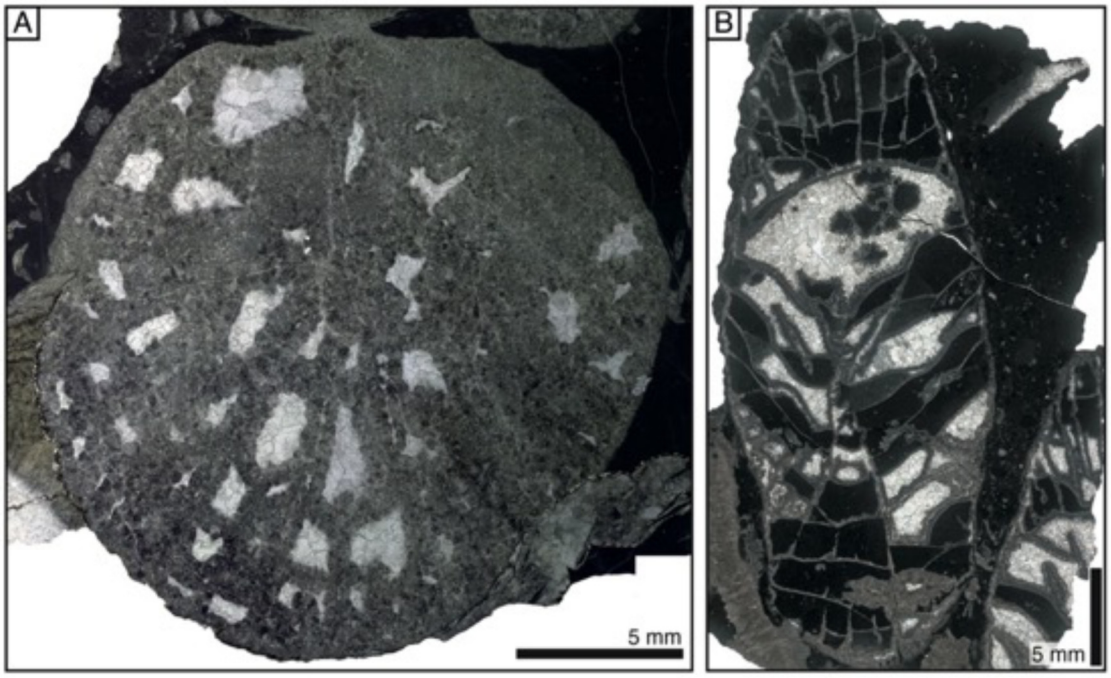

Fig. 30. *Phacelostylophyllum* mg. *martini* (Fromentel, 1860). A Transverse thin section of a branch of the specimen SB–205. B Longitudinal slightly oblique thin section of a branch of the specimen SB–231.

Genus ***Pinacophyllum*** (Frech, 1890)

Type species. *Pinacophyllum paralellum* (Frech, 1890) by monotypy (ICZN art. 68.3 as *Pinacophyllum* (?) *annulatum* (Reuss, 1855) was assigned with doubt to the genus *Pinacophyllum* by (Frech, 1890): p. 87).

Originally included species. *P. paralellum* (Frech, 1890), and *P.* ? *annulatum* (Reuss, 1855) with doubt.

Similarities and differences. This genus differs from *Phacelostylophyllum* (Melnikova, 1972) that has vesicular dissepiments and septal spines. *Pinacophyllum* differs from other phaceloid genera by its prominent character of complete tabulae.

Etymology. From *pinaco*: table in ancient Greek referring to the tabulae and *phyllum:* leaf in ancient Greek, a common ending in coral generic names.

Status. Available and valid.

***Pinacophyllum* sp**.

Figure 32

v. 2019 *Pinacophyllum?* sp. — Boivin, p. 252, fig. 10.30.

Material examined. 2 badly preserved colonies: SB–60 and SB–78/2.

Ages and localities of material. Upper Sinemurian from Serdrar reef and upper Sinemurian or lowermost Pliensbachian from Castle olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Phaceloid colonies. Septa compact, short, curved, in small number. Inner margin of septa is occasionally hook-shaped. Endotheca made of large tabuloid dissepiments and complete tabulae. Thick wall of unknown nature.

Dimensions. Diameter of branches 5 to 7 mm — Number of septa circa 6 septa — Thickness of the wall circa 0.5 mm.

Remarks. The very bad preservation made the identification very difficult. However, due to the original character of the endotheca another generic attribution is not considered plausible.

Similarities and differences. We have investigated the nominal species assigned to *Pinacophyllum.* Among them *Pinacophyllum conglomeratum* (Frech, 1889) is not an available name (ICZN art. 1.3.5). It was published as a *nomen nudum* as a species of *Amplexus* (?). One year later, Frech (1890) stated that the single sample of *Amplexus* (?) *conglomeratus* should be temporarily named *Pinacophyllum* sp. nov. All the other nominal species, such as *P. annulatum* (Reuss, 1855), *P. gracile* (Münster, 1841), *P. lejowae* (Roniewicz, 1974), *P. parviseptum* (Squires, 1956), *P. parallelum* (Frech, 1890), *P. peruvianum* (Stanley, 1994),
P. spizzensis (Tornquist, 1899), and *P. yunnanense* (Wu, 1977), whether or not they belong to the genus *Pinacophyllum*, have many more septa than our specimen.

Stratigraphic and geographic distribution. Upper Sinemurian — lower Pliensbachian from Morocco (High Atlas Mountains).

Genus ***Stylophyllopsis*** (Frech, 1890)

Type species. *Stylophyllopsis polyactis* (Frech, 1890) by subsequent designation (Diener, 1921).

Originally included species. *Stylophyllopsis polyactis* (Frech, 1890), *Stylophyllopsis zitteli* (Frech, 1890), *Stylophyllopsis rudis* (Emmrich, 1853), *Stylophyllopsis caespitosa* (Frech, 1890), *Stylophyllopsis mojsvari* (Frech, 1890), and *Stylophyllopsis lindstroemi* (Frech, 1890).

Similarities and differences. *Stylophyllopsis* differs from other solitary genera by its septal structure characterised by

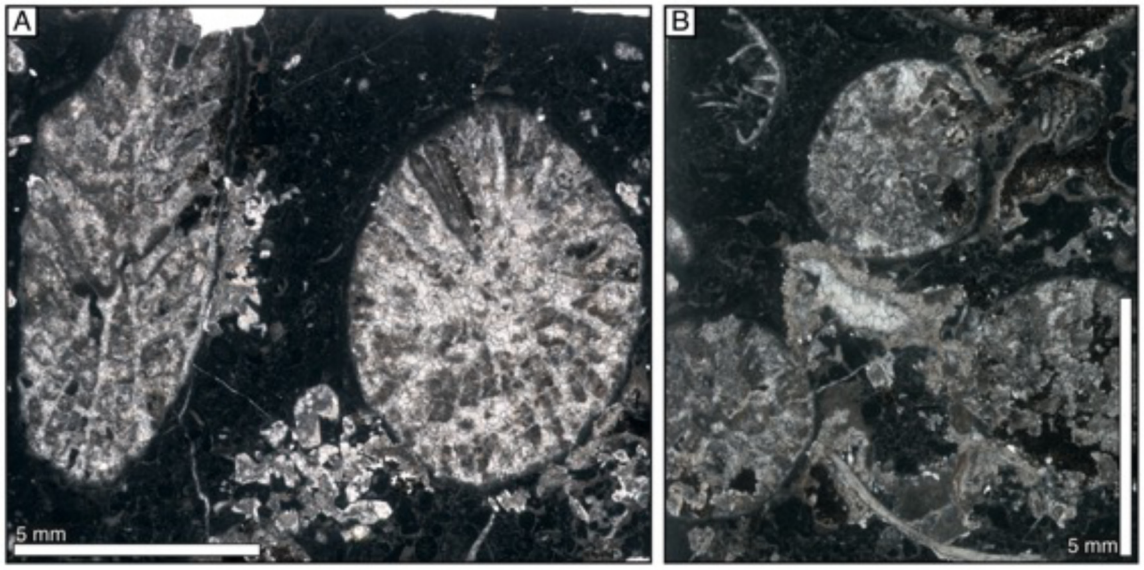

Fig. 31. *Phacelostylophyllum* mg. *suttonensis* (Duncan, 1867). A–B Transverse thin sections of branches of the specimen SB–170.

septal spines deriving from a microstructure dominated by thickening deposits;

- *Coryphyllia* (Cuif, 1975a) presents a mid-septal line and generally an elongated fossa.

- *Distichophyllia* (Cuif, 1975c) is characterised by a mid-septal line in zigzag, which is expressed in the morphology of thin septa.

- *Epismiliopsis* (Alloiteau, 1952) is very close to *Stylophyllopsis*, even possibly congeneric, but differs by the elongated fossa and the torsion of lateral septa.

- *Neorylstonia* (Vasseur *et al.*, 2019) has also poorly ornamented septa but a highly distinctive axial structure.

- Archaeosmiliid genera like *Archaeosmilia* (Melnikova, 1975a) or *Icaunhelia* (Beauvais, 1958) have strongly cuneiform septa and no septal spine.

- *Proleptophyllia* (Alloiteau, 1952) has highly ornamented septa with a dentate distal edge, and a narrow inter-septal space.

Etymology. From *stylos*: pillar and phyllos: leaf, and *opsis*: appearance of, in ancient Greek probably referring to the septal spines.

Status. Available and valid.

Stylophyllopsis cf. walliae (Duncan, 1867)
Figure 33

* 1867 *Montlivaltia walliae* sp. nov. — Duncan, p. 7, Pl. 8 figs. 5–7.

1867 *Thecosmilia plana* sp. nov. — Duncan, p. 17, Pl. 3 figs. 24–25.

1868 *Montlivaltia rugosa* sp. nov. — Duncan, p. 58, Pl. 14 figs. 1–3, Pl. 15 figs. 14, 16 and 17, Pl. 16 figs. 5–15.

1878 Montlivaltia rugosa "Wright" — Tomes, p. 187.

1884b *Montlivaltia walliae* Duncan — Tomes, p. 363.

1925 *Stylophyllopsis rugosa* (Duncan & Wright) — Straw, p. 351, fig. 1.1–1.5.

1936 Montlivaltia rugosa "Wright in Duncan" — Joly, p. 169.

1943 *Oppelismilia rugosa* (Duncan & Wright) — Vaughan & Wells, p. 155, fig. 32a.

1956 *Oppelismilia rugosa* (Duncan & Wright) — Wells, p. F395, fig. 290.1c.

1975 *Stylophyllopsis walliae* (Duncan) — Beauvais, p. 114, fig. 3.

1975 *Stylophyllopsis rugosa* (Duncan) — Beauvais, p. 114, fig. 4.

1975 *Stylophyllopsis walliae* (Duncan) — Turnšek, Seyfried, & Geyer, p. 135, Pl. 16 figs. 1–2.

1976 *Stylophyllopsis walliae* (Duncan) — Beauvais, p. 51, Pl. 8 figs 9–10, Pl. 10 figs. 6–7, Pl. 11 figs. 1–2, text-fig. 4–6.

1976 *Stylophyllopsis rugosa* (Duncan & Wright) — Beauvais, p. 54, pl. 11 fig. 6, text-fig. 10.

1986 *Stylophyllopsis walliae* (Duncan) — Beauvais, p. 6.

1991 Stylophyllopsis walliae (Duncan) — Negus p. 255 Table 1

1993 *Stylophyllopsis rugosa* (Duncan & Wright) — Roniewicz & Morycowa, fig. 2.7.

2001 *Stylophyllopsis rugosa* (Duncan) — Stolarski & Roniewicz, fig. 5.1–5.2.

cf 2002 *Stylophyllopsis* sp. *cf. S. rugosa* (Duncan & Wright) — Stolarski & Russo, p. 656, figs. 7–8.

v cf 2019 *Stylophyllopsis cf. walliae* (Duncan) — Boivin, p. 260, fig. 10.34.

Type designation. Holotype by monotypy, BRLSI n° 260 (collection Moore).

Type locality and horizon. Hettangian, Angulata chronozone, Brocastle deposits, Bridgend, South Wales, Great Britain.

Originally included material. Only the holotype.

Etymology. Hypothetically dedicated to Mrs. Wall (Duncan previously dedicated also a species to Mr. Wall: *Antillia walli* Duncan and Wall, 1865).

Material examined. 1 specimen: SB–207.

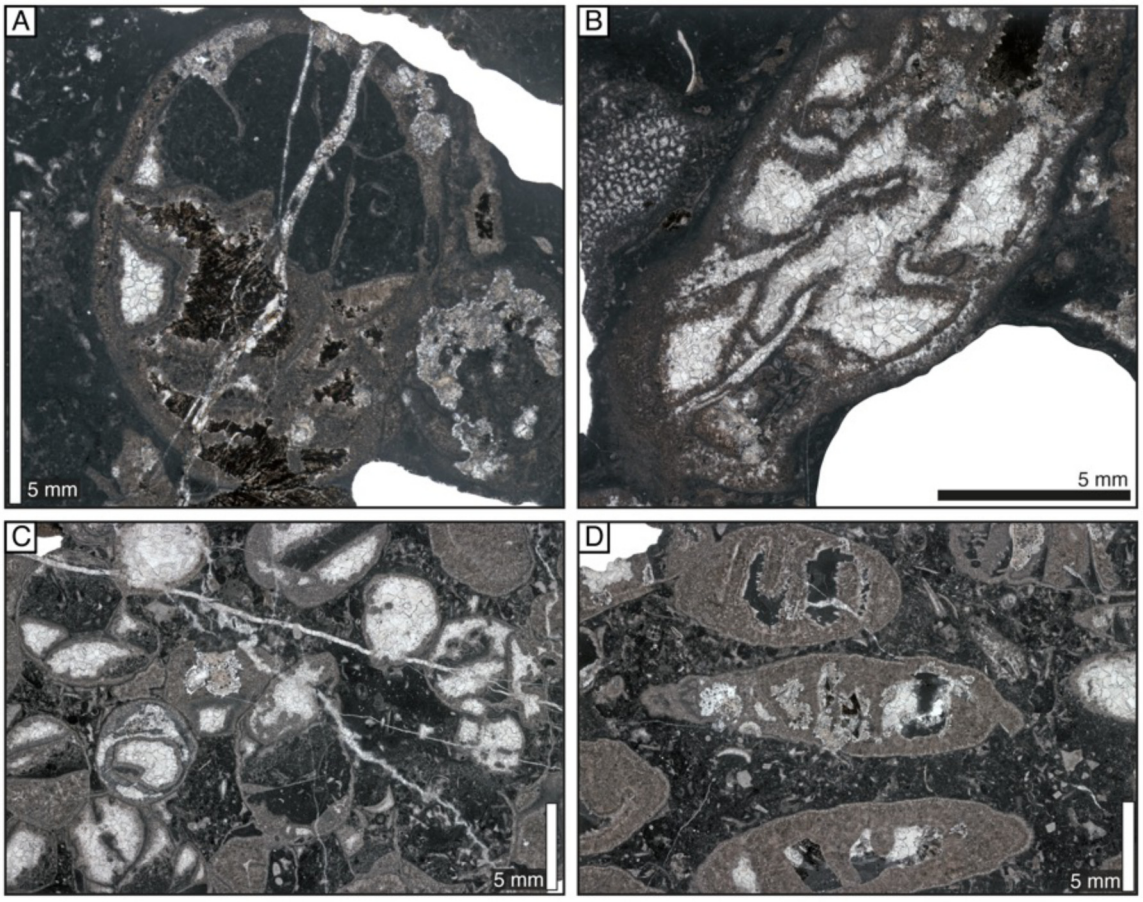

Fig. 32. *Pinacophyllum* sp. A Transverse thin section of the specimen SB–78/2. B Oblique thin section of the specimen SB–78/2. C Transverse thin section of the specimen SB–60. D Oblique thin section of the specimen SB–60.

Ages and localities of material. Upper Sinemurian from Serdrar reef, High Atlas Mountains, Morocco.

Description. Solitary coral, corallite circular or elliptical. Septa with stylophyllid structure, subcompact, free or sometimes joined, straight and thick. Septal apparatus organised in two size orders (perhaps three). Inner margin of septa characterised by dissociated free septal spines, which are projected in the lumen and produce a parietal papillose columella. Endotheca made of large dissepiments.

Dimensions. Calicular diameter circa 15–20 mm — Septal density 4 septa per 5 mm — Number of septa circa 46 septa.

Similarities and differences. The bad preservation of our specimen does not permit a firm identification. However, compared to the other nominal species of the genus *Stylophyllopsis* (Tab. 7), our specimen seems to be close to *Stylophyllopsis walliae* by its calicular diameter and its number of septa. Table 7 and Figure 34 suggest that the genus has been unreasonably split. We have, however, not the necessary population to solve this issue.

Stratigraphic and geographic distribution. Hettangian–Sinemurian from Belgium and Morocco, Hettangian from Great Britain, Sinemurian from Great Britain and Sicily, upper Sinemurian from Morocco, upper Sinemurian – Lower Pliensbachian from Spain.

Family **Thecosmiliidae** (Duncan, 1884)

Genus ***Vallimeandropsis*** (Beauvais, 1966a)

Type species. *Latomeandra davidsoni* (Edwards and Haime, 1851)a by original designation, p. 873.

Originally included species. Only the type species.

Similarities and differences. This genus differs from *Microphyllia* (Orbigny, 1849) that shows a pennular structure whereas septa of *Vallimeandropsis* display a montlivaltiid structure.

Etymology. From *vallis*: valley in Latin, *Maiandros*: Maeandros, a river of Anatolia famous for its meanders and *opsis*: appearance of, in ancient Greek referring to its meandroid morphology.

Status. Available and valid.

Vallimeandropsis davidsoni
(Edwards and Haime, 1851a)
Figure 35

* 1851a *Latomeandra davidsoni* sp. nov. — Edwards & Haime, p. 137, pl. 27 figs. 10, 10a.

1857 *Latimœandra davidsoni* Edwards & Haime – Edwards & Haime, p. 549.

1861 Latimœandra davidsoni Edwards & Haime — Fromentel, p. 161.

? *1865 Latomaeandra davidsoni* Edwards & Haime — Eichwald, p. 145.

1882 Latimœandra davidsoni Edwards & Haime — Tomes, p. 426.

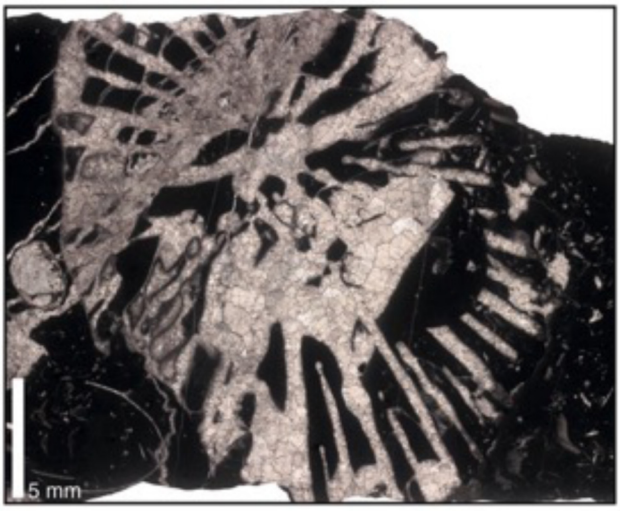

Fig. 33. –*Stylophyllopsis cf. walliae* (Duncan, 1867). Transverse section of specimen SB–207.

non 1885 *Latimæandra davidsoni* Edwards & Haime — Koby, p. 248, Pl. 73 fig. 2.

non? 1885 *Latimæandra curtata* (Etallon) — Koby, p. 223, Pl. 69 figs. 1–3.

1888 Latimaeandra davidsoni Edwards & Haime — Schlippe, p. 83.

? 1888 *Latimaeandra davidsoni* Edwards & Haime — Meyer, p. 35, Pl. 4 fig. 1.

1890 Latimæandra davidsoni Edwards & Haime — Tomes, p. 304.

non? 1905 *Latimaeandra curtata* (Etallon) — Koby, p. 105, Pl. 16 fig. 2.

? *1907 Latimæandra davidsoni* Edwards & Haime — Koby, p. 31.

? *1955a Microphyllia davidsoni* (Edwards & Haime) — Geyer, p. 346.

? *1955b Microphyllia davidsoni* (Edwards & Haime) — Geyer, p. 205.

1957 Brachyseris davidsoni (Edwards & Haime) — Alloiteau, p. 313.

1957 Microphyllia davidsoni (Edwards & Haime) — Frajová, p. 52.

non 1958 *Microphyllia cf. davidsoni* (Edwards & Haime) — Alloiteau, p. 92, Pl. 29 figs. 4, 5, 6.

non? 1958 *Isastraea davidsoni* (Edwards & Haime) — Alloiteau, p. 44, Pl. 5 fig. 6, Pl. 16 fig. 1; Pl. 19 fig. 5, Pl. 23 fig. 5.

non 1964 *Microphyllia curtata*? (Etallon) — Beauvais, p. 250, Pl. 35 fig. 1.

v 1966a *Vallimeandropsis davidsoni* (Edwards & Haime) — Beauvais, p. 873, Pl. 36 fig. 1, Pl. 37 fig. 3.

1970 Vallimæandropsis davidsoni (Edwards & Haime) — Beauvais, p. 61.

1971 Vallimaeandropsis davidsoni (Edwards & Haime) — Beauvais, p. 2.

? 1980 *Brachyseris davidsoni* (Edwards & Haime) — Ljuljeva & Permjakov, p. 95, Pl. 20 figs. 7, 8.

1986 *Microphyllia lineata* sp. nov. — Beauvais, p. 58, fig. 2, Pl. 14 fig. 2.

1993 *Vallimeandropsis davidsoni* (Edwards & Haime) — Pandey & Fürsich, p. 24, Pl. 11 fig. 1.

v. 2010 *Vallimeandropsis davidsoni* (Edwards & Haime) — Lathuilière, www.corallosphere.org with figures.

v. 2011 *Microphyllia*? *lineata* Beauvais — Lathuilière, p. 540, Pl. III figs.1–3.

? 2015 *Vallimeandropsis davidsoni* (Edwards & Haime) — El-Sorogy & Al-Kahtany, p. 100, fig. 5.H–I.

v. 2018 *Vallimeandropsis lineata* (Beauvais) — Vasseur, p. 370-371, fig. 3.107.

v. 2019 *Vallimeandropsis lineata* (Beauvais) — Boivin, p. 262, figs. 10.35–10.36.

Remarks. After an assignation to the genus *Brachyseris* in 1957, Alloiteau (1958) has simultaneously attributed the species *Latomeandra davidsoni* (Edwards & Haime, 1851)a to *Isastraea* (p. 44) and *Microphyllia* (p. 92). These two names, however, correspond to different taxa: *Microphyllia cf. davidsoni* (Edwards and Haime, 1851a) in Alloiteau (1958) is a badly preserved colony, which can be possibly referred to *Microphyllia*, when *Isastraea davidsoni* (Edwards & Haime, 1851a) in Alloiteau (1958) shows a good thin transverse section (Pl. 16 fig. 1) in which the montlivaltiid microstructure is clearly demonstrated. We attribute this section figured in Alloiteau (1958) to the cerioid genus *Isastrea* (Edwards and Haime, 1851b). It has been considered as a new species by Beauvais (1966a): *Vallimeandropsis vongohensis*. The homogeneity of the syntypes of the latter species is not demonstrated.

Latimæandra davidsoni Edwards & Haime in (Koby, 1885) was also erected as a new species: *Microphyllia pulchella* (Beauvais, 1966b).

Type designation. Neotype, designated by Beauvais, 1966a: p. 873 Pl. 36 fig. 1 and Pl. 37 fig. 3, NHMUK R 21152, also photographed in Corallosphere (Lathuilière, 2010).

Type locality and horizon. Bajocian of Crickley (near Cheltenham, Great Britain).

Originally included material. Only the lost holotype.

Etymology. Dedicated to Thomas Davidson, a famous Scottish palaeontologist.

Material examined. 3 colonies: SB–143, SB–314 and SB–335.

Ages and localities of material. Upper Sinemurian from Serdrar reef and upper Sinemurian or lowermost Pliensbachian from Castle olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Meandroid colonies. Intracalicular budding producing corallites in a single row within a valley and united by a lamellar linkage (Fig. 35E). Corallites distributed in sub-parallel series often curved or slightly sinuous. Collines tectiform without ambulacrum. Septa sub-confluent or confluent on both sides of collines, joined, or sometimes free, straight or curved, sub-compact. Montlivaltiid septal structure with lateral faces of septa granulated. No pennulae. Microstructure trabecular and slight trabecular detachment at the inner margin of septa projected in the axial region. Columella parietal. Septal density highly variable inside valleys. Endotheca made of dissepiments including vesicular dissepiments.

Table 7. Dimensions of type material of *Stylophyllopsis* nominal species. Diameters are rounded to the nearest half-millimetre. F. Dimensions of figured material in absence of type specimen (*S. guettardi*: figuration from Lejeune, 1935). H. Dimensions of the holotype. L Dimensions of the lectotype. TS. Dimensions of the type series. S Dimensions of the syntype(s). * Dimensions estimated from figures or photographies. Remark: *Stylophyllopsis pontebbanae* (Volz, 1896) is not included in the table because it has been reassigned to *Pontebbastraea* (Roniewicz & Michalik, 2002), a junior synonym of *Remismilia* (Beauvais, 1972) according to (Roniewicz, 2010b). *Stylophyllopsis laxa* (Fromentel & Ferry, 1867) is considered a junior synonym of *S. fritillus* according to Vasseur & Lathuilière (2021). *S. rugosa* (Duncan, 1868) is regarded as a junior synonym of *S. walliae* (Duncan, 1867) according to Beauvais (1986).

Nominal species		Diameter	Number of septa	Septal density
S. bobrovensis (Roniewicz & Michalik, 1998)	*S*	20–25 mm	circa 80	?
S. bovista (Vasseur & Lathuilière, 2021)	*TS*	20–33 mm	60–70	4–5 per 5 mm
S. brevis (Duncan, 1867)	*S*	4.5–6 mm	32	?
S. caespitosa (Frech, 1890)	*H*	5–7 mm	circa 16	?
S.? consobrina (Fromentel & Ferry, 1866)	*S*	10–11 mm	136	?
S. denticulata (Fromentel & Ferry, 1866)	*S*	29–38 mm*	110–192* (approx.)	10 per 5 mm*
S. elchabirensis (Beauvais, 1986)	*H*	9.5 mm	circa 43	?
S. fritillus (Fromentel & Ferry, 1866)	*L*	17 mm*	circa 40*	6 per 5 mm*
S. gracilis (Stanley, 1994)	*H*	8–15 mm	62–68	8–10 per 5 mm
S. guettardi (Blainville, 1830)	*F*	16–28 mm*	circa 80–90*	6–12 per 5 mm
S. karauldyndalaensis (Melnikova, 1972)	*H*	30–40 mm	56–96	?
S. lindstromi (Frech, 1890)	*L*	8 mm*	40*	3 per 1 mm*
S. media (Roniewicz, 1974)	*TS*	9–11 mm	40–45	?
S. minisculus (Deng, 2006)	*S?*	4—6 mm	40	
S. mojsvari (Frech, 1890)	*S*	6 mm	60–70	?
S. mucronata (Duncan, 1868)	*L*	30 mm	78	?
S. murchisoniae (Duncan, 1867)	*L*	10–15 mm	60–90?	?
S. paradoxum (Frech, 1890)	*S*	7-42.5 mm (mean around 15–20)*	25–70*	3-6 per 5mm*
S. patula (Duncan, 1868)	*L*	16–19 mm	96	?
S. polyactis (Frech, 1890)	*L*	circa 44 mm*	circa 150–160*	?
S. praenuntians (Volz, 1896)	*H*	12–18 mm	82	4–5 per 1 mm
S. punctulum (Fromentel & Ferry, 1867)	*L*	20 mm	216	18 per 5 mm*
S. ramosa (Roniewicz, 1989)	*H*	10 mm	41	?
S.? rhodana (Fromentel & Ferry, 1869)	*S*	13 mm	106	?
S. romerloana (Volz, 1896)	*S*	3–6 mm	16–20	?
S. rudis (Emmrich, 1853)	*S*	?	20	?
S. sinemuriensis (Orbigny, 1850)	*S*	24–25 mm	circa 79*	?
S. sp. in (Beauvais, 1986)		25–35 mm	circa 130	?
S.? spinigera (Fromentel & Ferry, 1867)	*S*	14–25 mm	77–96	?
S. thaugyinensis (Gregory, 1930)	*?*	4–9 mm	30–60	?
S. tenuispinum (Frech, 1890)	*S*	18–22 mm*	circa 92*	3–4 per 2 mm*
S. timoricus (Vinassa de Regny, 1911)	*H*	30 mm	circa 96	?
S. veracolumella (Vasseur & Lathuilière, 2021)	*TS*	16–18 mm	circa 62	3–4 per 2 mm
S. vetusum (Beauvais, 1986)	*H*	17–20 mm	circa 120	4–7 per 2 mm
S. victoriae (Duncan, 1868)	*L*	34–51.5 mm	110–135	?
S. walliae (Duncan, 1867)	*L*	17–18 mm	46	?
S. zitteli (Frech, 1890)	*L*	16–17.5 mm*	34	4 per 5 mm*

Dimensions. Valley width 2.5 to 5 mm — Colline width 0.3 to 0.7 mm — Septal density 4 to 8 septa per 2 mm — Distance between trabecular axes 120 to 280 µm.

Stratigraphic and geographic distribution. Upper Sinemurian – Lowermost Pliensbachian from Morocco, Middle and upper Toarcian from Morocco, Bajocian from England, Germany?, Bathonian from France? and India, Upper Jurassic from Crimea?, Portugal? and Saudi Arabia?, Tithonian-Berriasian from Czech Republic?

Family **Incertae Sedis**

Genus indet.

Similarities and differences. This genus differs from other cerioid genera:

— *Rhaetiastraea* Roniewicz, 1974 that has a papillose or parietal columella, the size orders of the septal apparatus better ordered in length and thickness; *Rhaetiastraea* as many other actinastreid genera has often S3 in contratingent junction;

— *Bussonastrea* Beauvais, 1965 that has a characteristic septal budding;

— *Edwardsastraea* (Roniewicz, 1970) that has a papillose columella;

— *Enallocoenia* (Orbigny, 1849) that has an extracalicular budding and straight septa;

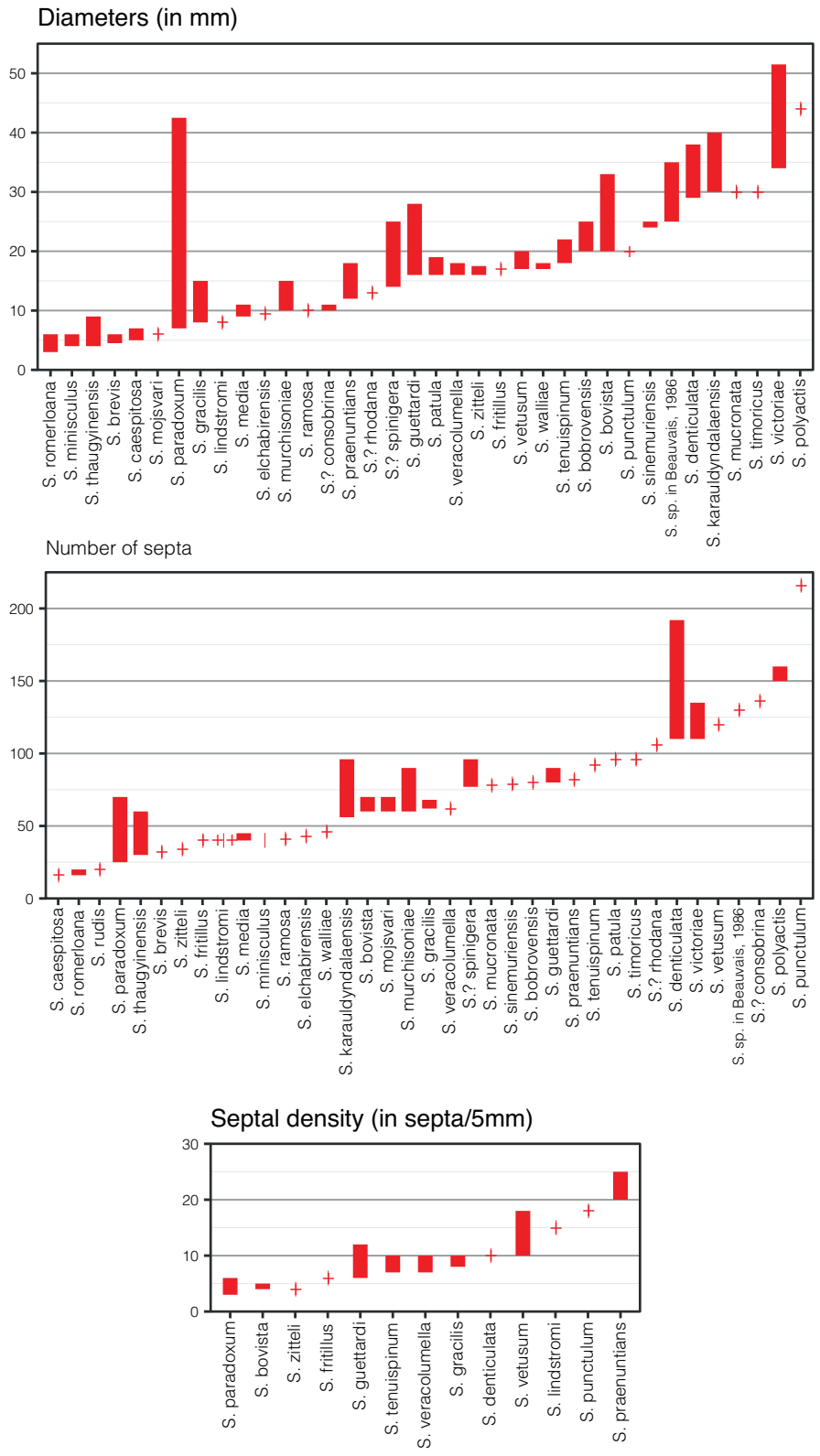

Fig. 34. Plots of dimensions of the type material of *Stylophyllopsis* nominal species presented in Table 7.

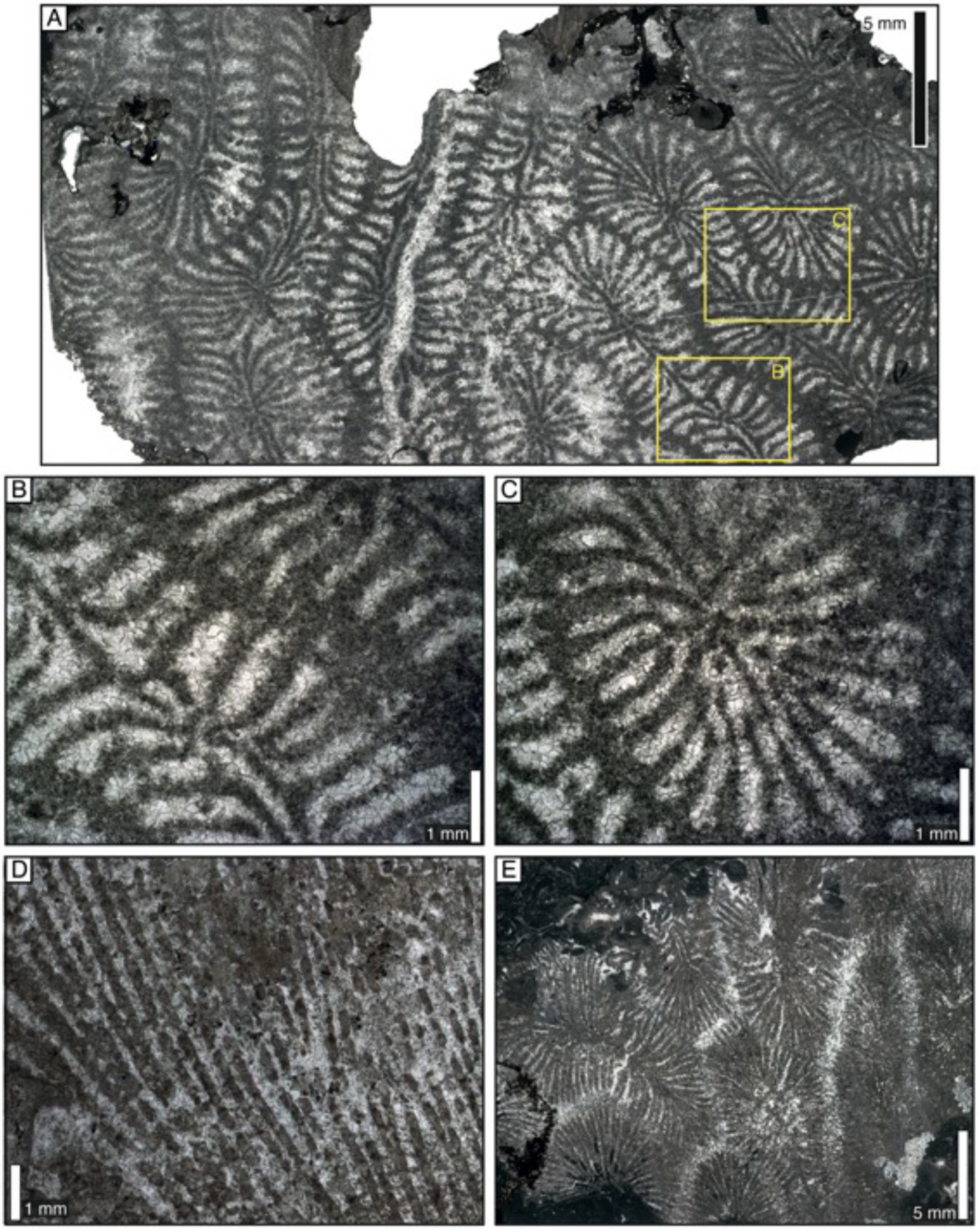

Fig. 35. *Vallimeandropsis davidsoni* (Edwards & Haime, 1851a) A Transverse thin section of the colony SB–335. B–C Enlargements of A. D Longitudinal thin section of the colony SB–143. E Transverse thin section of the colony SB–143.

— *Pseudodiplocoenia* (Alloiteau, 1958) that has joined septa and a columella of septal origin;

— *Sakalavastraea* (Alloiteau, 1958) that has a parietal columella made of the junction of major septa;

— *Septastraeopsis* (Alloiteau, 1953) that has a septal budding and septa joined to columella;

— *Toechastrea* (Volz, 1896) that has trabecular axes perpendicular to the mediosepta plan in the peripheral part and that tend to alternate and grow obliquely inward near the columella;

— *Tropiastrea* (Cuif, 1967) with its pennular structure characterised by meniana directed upward.

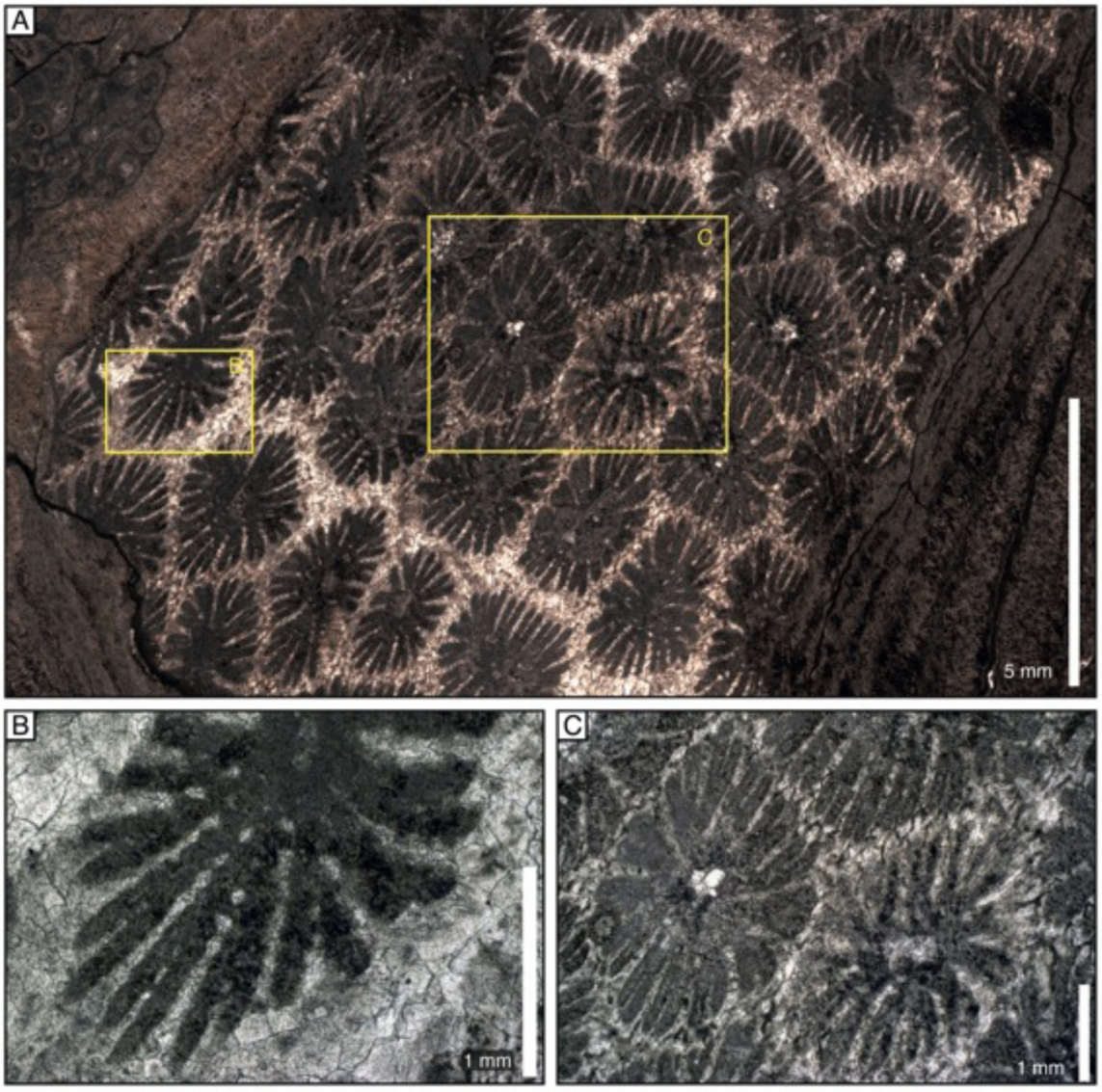

Fig. 36. Gen. indet. sp. A transverse section of specimen SB–210/2. B–C Enlargement of A.

Gen indet. sp.

Figure 36

non 1976 *Toechastraea pachyphylla* sp. nov. — Cuif, p. 146, Pl. 16 figs. 3–4.

? 1987 *Toechastraea pachyphyllia* Cuif — Turnšek & Ramovš, p. 41–42, Pl. 3 figs. 5–6.

? 1997 *Toechastraea pachyphyllia* Cuif — Turnšek, p. 207.

v 2019 Gen indet. sp. — Boivin, p. 208, fig. 10.13.

Material examined. 1 colony: SB–210/2.

Ages and localities of material. Upper Sinemurian from Serdrar reef, Amellagou Region, High Atlas Mountains, Morocco.

Description. Colony cerioid. Probably growing by intracalicular budding. Corallite polygonal or elliptical. Septa compact except the inner margin, free, uncommonly joined, confluent or not confluent, curved. Septal apparatus organised in three size orders, not always easy to distinguish (particularly between S1 and S2). Lateral margin of septa ornamented by rounded granules or slightly pointed ones (Fig. 36B). Trabeculae are dissociated at inner margin of septa. Well delimited styliform columella. No pali. Endotheca not visible. Septothecal wall in zigzag.

Dimensions. Calicular great diameter 2.58 to 3.13 mm — Calicular small diameter 2.36 to 2.56 mm — Thickness of the wall 0.22 to 0.25 mm — Distance from corallite to corallite 2.19 to 2.33 mm —Septal density 5 to 6 septa per 1 mm — Trabecular density 3 to 4 per 0.5 mm.

Remarks. Our specimen is very close to the material figured by Turnšek & Ramovš (1987) (also figured in Turnšek, 1997) under the species name *Toechastraea pachyphyllia*. However, the Slovenian specimen, like ours, does not allow the observation of the typical ornamentation of lateral faces of septa and in particular the typical granules, well preserved of the type material of *Toechastraea pachyphyllia* (Cuif, 1976). In both

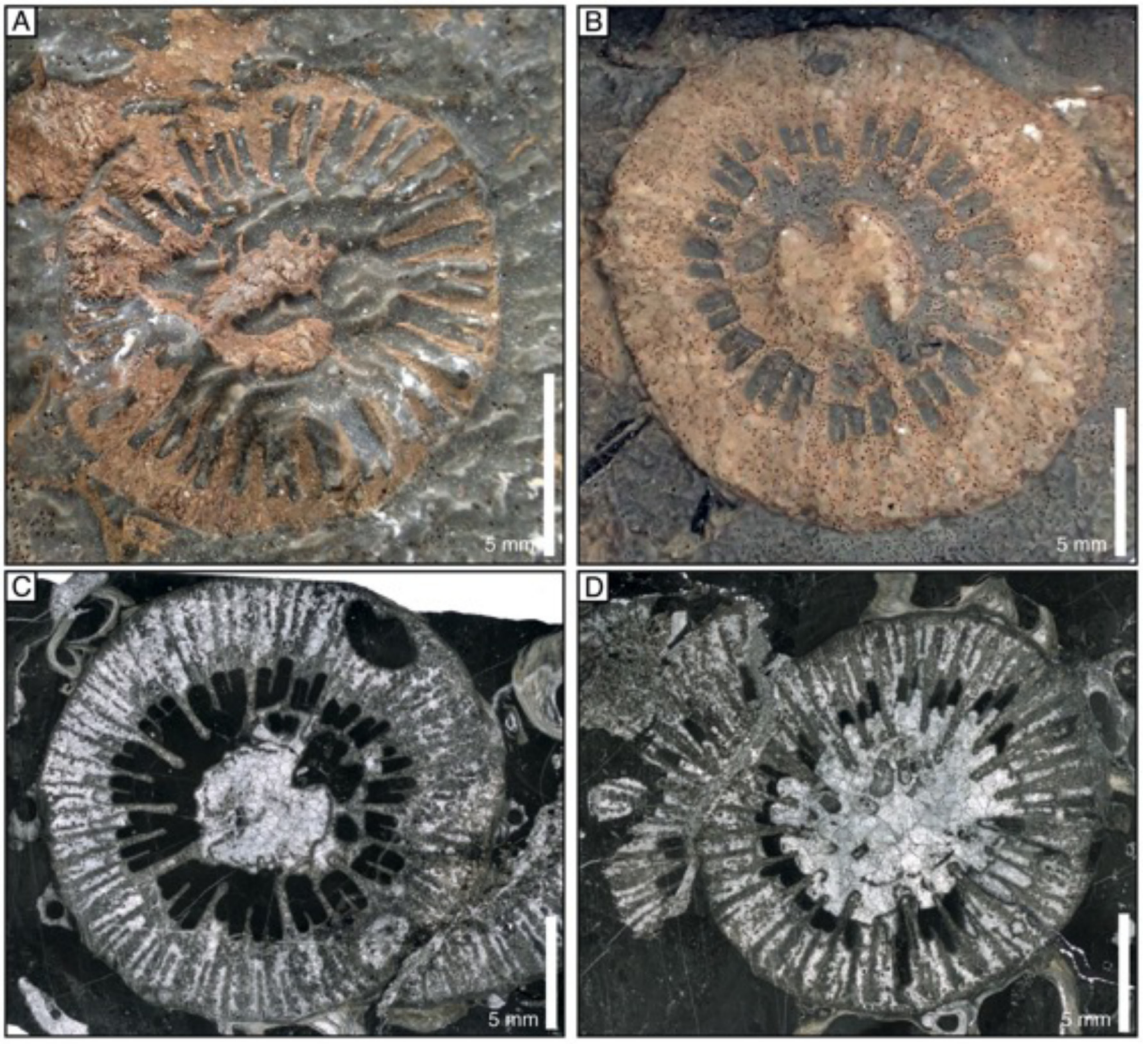

Fig. 37. *Neorylstonia pseudocolumellata* (Beauvais, 1986) A Natural transverse section of the specimen SB–166. B Natural transverse section of the specimen SB–236. C–D Transverse thin section of the specimen SB–236. Section C is more distal (12 mm) than section D.

cases also, the interseptal space is much wider than in *Toechastraea pachyphyllia* and septal junctions are not observed.

Stratigraphic and geographic distribution. Norian from Slovenia?, Sinemurian from Morocco (High Atlas Mountains).

Genus ***Neorylstonia*** (Vasseur *et al.*, 2019)

nomen novum pro *Mesophyllum* (Beauvais, 1986) non (Schlüter, 1889)

Type species. *Mesophyllum pseudocolumellatum* (Beauvais, 1986) by original designation.

Originally included species. Only the type species.

Similarities and differences. This genus differs from other solitary genera by its very characteristic axial structure: the pseudocolumella (see Vasseur *et al.*, 2019 for a precise definition).

Etymology. From *neo*: new in ancient Greek, and *Rylstonia* a very similar Palaeozoic rugosan genus.

Status. Available and valid.

Neorylstonia pseudocolumellata (Beauvais, 1986)
Figure 37

*v 1986 *Mesophyllum pseudocolumellatum* sp. nov. — Beauvais, p. 20, Pl. 4, fig. 1a–1b.

v. 2018 *Neorylstonia pseudocolumellata* (Beauvais) — Vasseur, p. 259-260, fig. 3.63.

v. 2019 *Neorylstonia pseudocolumellata* (Beauvais) — Vasseur *et al.*, p. 12–17, fig. 2–6.

v. 2019 *Neorylstonia pseudocolumellata* (Beauvais) — Boivin, p. 224–225, fig. 10.20.

v. 2021 *Neorylstonia pseudocolumellata* (Beauvais) — Vasseur & Lathuilière, p. 1234, fig. 32.

Type designation. Holotype by original designation of Beauvais (1986: p. 20, pl. 4 fig. 1a,b) MNHN.F.R11604, Menchikoff collection.

Type locality and horizon. Lower Jurassic from Beni Tadjit, High Atlas Mountains, Morocco.

Originally included material. Four paratypes: MNHN.F. A30500, MNHN.F.R11605 (Pl. 4 fig. 1c–d), MNHN.F.R11606 (Pl. 4 fig. 1e) & MNHN.F.R11607 (Pl. 4 fig. 1f).

Etymology. From *pseudocolumella* referring to the characteristic axial structure of the genus.

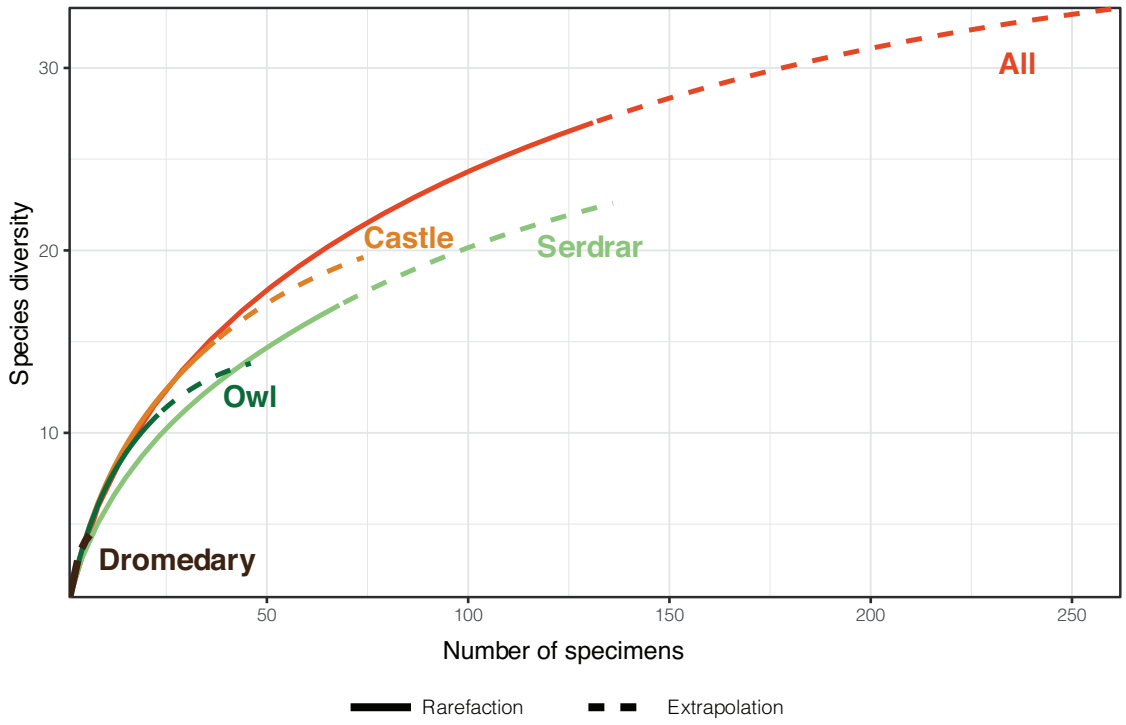

Fig. 38. Rarefaction curves of the taxa from the different studied localities (*i.e.*, the Dromedary biostrome, the Serdrar reef, the Castle olistolith and the Owl olistolith), in comparison to the global curve that takes into account the whole set of assemblages described in the present study.

Material examined. 5 specimens: SB–164, SB–166, SB–206, SB–236 and SB–238 and 1 uncertain specimen: SB–241.

Ages and localities of material. Upper Sinemurian from Serdrar reef, upper Sinemurian or lowermost Pliensbachian from Castle olistolith and lower Pliensbachian from Owl olistolith, Amellagou Region, High Atlas Mountains, Morocco.

Description. Solitary coral. Corallum ceratoid. Corallite circular to sub-circular. Costosepta straight or slightly curved, free, compact, occasionally rhopaloid. Radial elements are commonly arranged in three distinct size orders with different length and width in transverse sections but S1 and S2 are occasionally indistinct because of similar sizes. Some first-order septa (S1) rarely reach the axial structure but in most cases the inner edge abruptly dips in the fossa. Lateral faces and distal edge are smooth. No palus. Axial structure present, in the form of a Rugose-like calicular boss consisting of septa and endotheca — a pseudocolumella according to Edwards & Haime (1848) and later to Berkowski & Weyer (2012). This pseudocolumella presents different morphologies during the polyp life, giving the fossils a very characteristic aspect in transverse section. In the main cases, hexameral symmetry can be recognised. The superimposed bilateral symmetry is evidenced by the spatial organization of the axial structure. Endotheca abundant, made of tabular dissepiments regularly arranged in the axial zone. Parathecal wall. Paratheca is continuous with the dissepiments. Synapticulae absent.

Dimensions. Calicular great diameter 14.5 to 20.5 mm — Calicular small diameter 12.5 to 20 mm — Number of septa 40 to 50 septa — Septal density 5 to 7 septa per 1 mm.

Stratigraphic and geographic distribution. Sinemurian – Pliensbachian from Morocco (Middle and High Atlas Mountains), Pliensbachian from Italy.

4 Results & conclusion

The distribution of the different specimens given in Table 3 was considered in order to assess the representativeness of our samples, from the 4 localities studies, *i.e.*, the Dromedary biostrome, the Serdrar reef, the Castle olistolith and the Owl olistolith. The rarefaction curves (Fig. 38) of the three main localities (Serdrar, Castle and Owl reefs) show a similar relationship between the specific richness and the number of specimens. The Serdrar reef, despite its large size, also compared to the others, is a little different and, according to the global curve, is approaching the maximum number of taxa more quickly. The Dromedary biostrome, the most ancient coral-bearing outcrop, due to its small size, is not representative of the real diversity of the corresponding time.

Figure 39A illustrates the distribution of the studied specimens according to their colonial arrangement. It demonstrates not only the important proportion of cerioid and solitary corals but also the occurrence of significant proportions of thamnasterioid and meandroid forms. In term of species, as shown in Figure 39B, the proportion of cerioid species is lower than expected from the Figure 39A. By contrast, the proportion of phaceloid species is significantly higher when compared to the proportion of phaceloid ones.

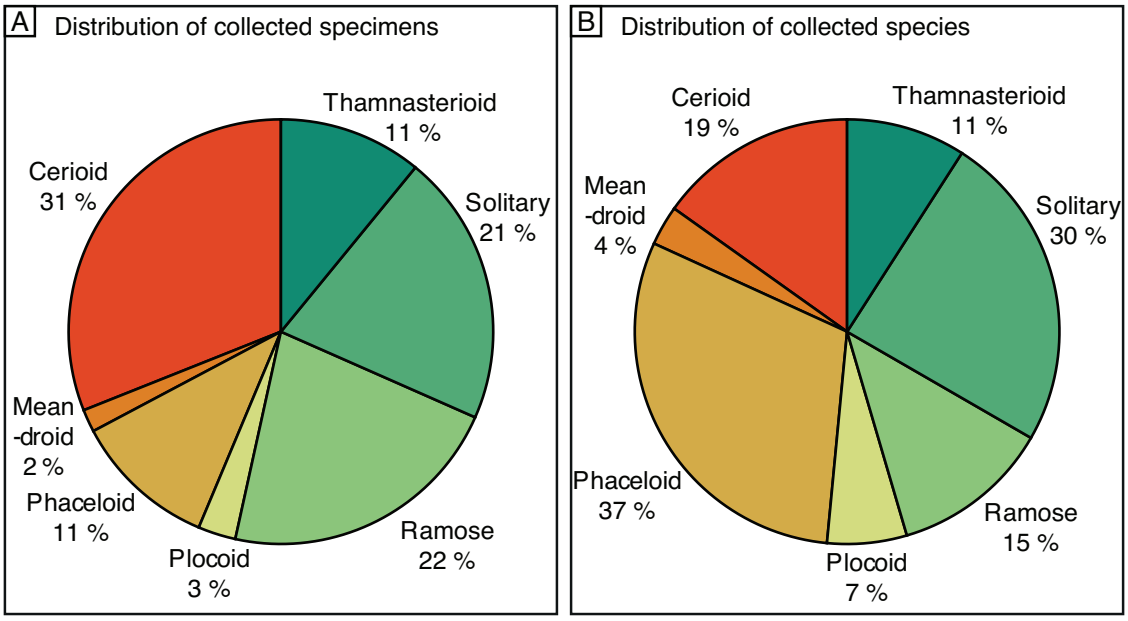

Fig. 39. A Distribution of collected specimens from the different studied localities (*i.e.*, the Dromedary biostrome, the Serdrar reef, the Castle olistolith and the Owl olistolith), according to their colonial arrangement. B Distribution of collected species from the different studied localities according to their colonial arrangement.

The high proportion of solitary forms remains strong for species and individuals.

The proportion of colonial arrangements among localities, is illustrated in Figure 40A. It can also be viewed in terms of chronology, from the oldest Dromedary biostrome (?Hettangian-Sinemurian) to the youngest Owl olistolith (lower Pliensbachian). It is important to note that Serdrar reef (upper Sinemurian) and Castle olistolith (upper Sinemurian or lowermost Pliensbachian) could be synchronous or even age-reversed. However, as already mentioned, the Dromedary biostrome cannot be reliably interpreted due to its low sampling. The Serdrar reef shows a high proportion of cerioid specimens while the proportion of solitary specimens is rather low. Contrastingly, the Owl olistolith exhibits a low proportion of cerioid specimens compensated by solitary ones. In some regards, the Castle olistolith presents intermediate values between the Serdrar reef and the Owl olistolith, but with a higher ratio of phaceloid specimens than the other two localities.

The Figure 40B complements the above results and provides some details on the specific compositions of the colonial arrangements within the different outcrops. Except for the Dromedary biostrome, because of the low number of samples, the proportions of solitary and cerioid species remain stable between all localities, while the proportion of solitary and cerioid specimens varies (see Fig. 40A). Finally, a great homogeneity is observed between the distributions of the colonial arrangements of Serdrar reef and Castle olistolith. In contrast, the Owl olistolith is characterised by a higher proportion of thamnasterioid species and a lower proportion of phaceloid species.

To summarize, the present study was conducted in the Amellagou Region in Moroccan High Atlas Mountains. More precisely concern the Dromedary biostrome (?Hettangian–Sinemurian), the Serdrar reef (upper Sinemurian), the Castle olistolith (upper Sinemurian or lowermost Pliensbachian) and the Owl olistolith (lower Pliensbachian).

Thanks to this new taxonomic assessment, the last appearance datum of the several genera has been changed, namely *Chondrocoenia*, *Parastraeomorpha, Araiophyllum, Paracuifia, Pinacophyllum*, and possibly *Paravolzeia*. The first appearance datum of *Proleptophyllia, Vallimeandropsis,* and possibly *Lochmaeosmilia* has also been revised. These modifications equally apply to several species (*cf.* Tab. 3). The present study, devoted solely to the lower Liassic of Morocco, fills a gap between Upper Triassic and upper Liassic records. In addition, it completes the recent data of Vasseur & Lathuilière (2021) for the Pliensbachian thanks to the data from the owl Olistolith. This study gives a very important indication that, although the Pliensbachian appears to be the best-represented stage of the Early Jurassic, its fossil record is still far from complete. Some Lazarus taxa known from the Triassic and Pliensbachian remain absent in the fossil record from Hettangian and, to a lesser degree now, from the Sinemurian. Therefore, we assume that the absence of these taxa is only due to the poor preservation of coral environments during these periods. This assumption is reinforced by the fact that several new occurrences correspond to a single specimen.

We now have new data to question the relative severity of the end-Triassic crisis in comparison to the Pliensbachian–Toarcian crisis. In this reassessment, the potential continuity of genera from the Triassic to the Jurassic should be re-evaluated. For instance, is there an evolutionary gap between the Triassic *Thamnasteriamorpha* and the Jurassic *Periseris*? Is *Chondrocoenia* so far from Jurassic actinastreids (*e.g.*, *Allocoenia, Allocoeniopsis, Stephanastrea)*? At the family level, the structure of the Triassic distichophyllid Reimaniphylliidae should be compared with that of the Jurassic montlivaltid

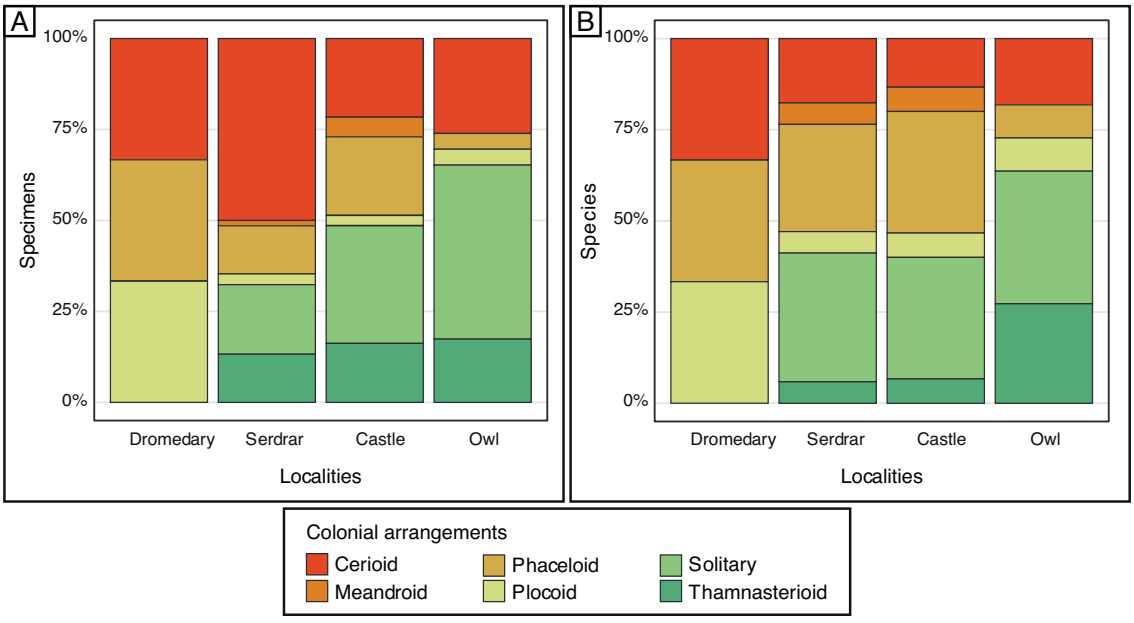

Fig. 40. A Distribution of collected specimens according to their colonial arrangement and split by their different studied localities (*i.e.*, the Dromedary biostrome, the Serdrar reef, the Castle olistolith and the Owl olistolith), B Distribution of collected species from the different studied localities, according to their colonial arrangement t and spitted by their different studied localities.

Thecosmiliidae. Could these two structures, up to now considered as assuredly separated, also be considered as the two end-members of an evolutionary continuum? In this regard, the Triassic material described by Deng & Zhang (1984a) from China provides questioning evidences for an early onset of the montlivaltid structure (notably Pl. 2 fig. 1b and 4b, Pl. 3 figs. 1c and 3b).

The new data provides here also new light on the question of the relationship between corals and zooxanthellae in the post-end-Triassic crisis context. In particular, the hypothesis of the loss of symbiosis (Rosen, 2000) can be tested. A significant relationship between colonial structures and photosymbiosis is established (*e.g.*, Coates & Oliver, 1973; Coates & Jackson, 1987). On the above basis, we consider that the occurrence of highly integrated forms, such as thamnasterioid and meandroid colonial structures in our outcrops, is a strong argument for the existence of a photosymbiosis. Presently, we know only one exception to this principle, with the thamnasterioid troglodytic species *Leptoseris troglodyta* Hoeksema, 2012 which has lost its zooxanthellae (Hoeksema, 2012). A further strong argument for the existence of corals with zooxanthellae as early as the lowermost Jurassic is the existence of two species demonstrating a morphological change from lamellar to ramose that cannot be explained without the photosymbiosis. Indeed, *Hispaniastraea murciana* and *Chondrocoenia clavellata* show this morphological change that is known in the recent zooxanthellate coral *Synaraea convexa* (Verrill, 1864) (Jaubert, 1977). However, this does not imply that all corals in this epoch were zooxantellate. It can be considered that a significant proportion of solitary forms were possibly not. The complexity of the evolutionary interactions between different coral genera and zooxanthellae lineages, and their effect on the efficiency of carbonate production remains unknown.

Finally, the investigation of Moroccan Liassic outcrops has significantly improved our knowledge of corals' evolution. There is still much scope for further explorations to take advantage of the high quality and quantity of Liassic coral-bearing outcrops in Morocco. However, the new knowledge from the Moroccan fossil record needs to be completed by other Liassic localities, both from Tethys and Panthalassa, to reach the global picture of coral evolution during the Liassic.

Supplementary material

Supplementary Table 1. List of species with their number by localities (including doubtful assignations) and their colonial structures. This table is a reorganised version of Table 3.

Supplementary Table 2. Measurements of *Lepidophyllia* (*Heterastraea*) *microcalix* sp. nov specimens used for Figure 27 principal component analysis.

The Supplementary Material is available at https://www.bsgf.fr/10.1051/bsgf/2024027/olm.

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